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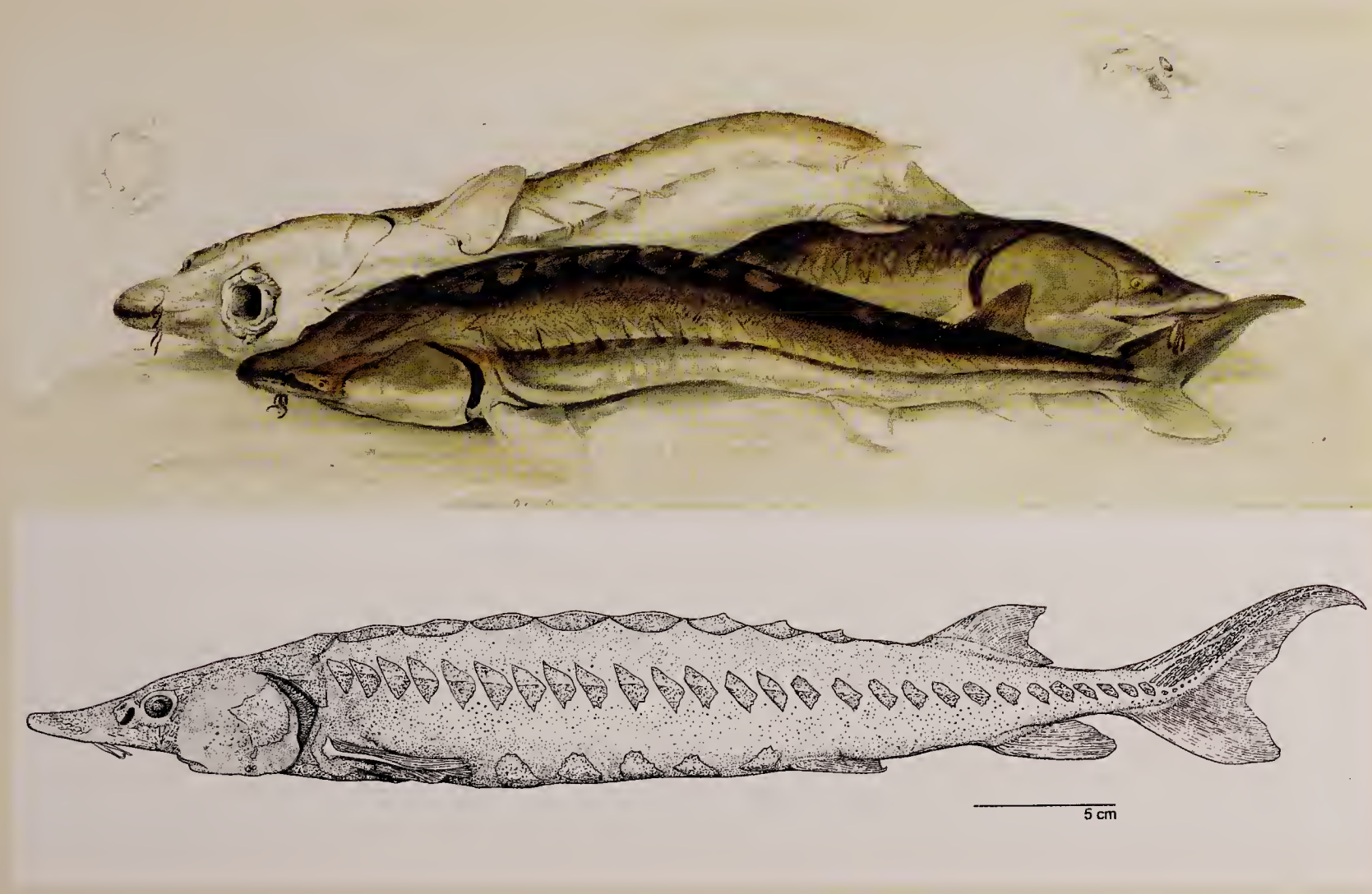
NO. 3

Skeletal Anatomy of the Shortnose Sturgeon, *Acipenser brevirostrum* Lesueur, 1818, and the Systematics of Sturgeons (Acipenseriformes, Acipenseridae)

Eric J. Hilton
Lance Grande
William E. Bemis



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Cover: *Acipenser brevirostrum* Lesueur, 1818. **Above**, an unpublished color illustration of the shortnose sturgeon made by Charles-Alexandre Lesueur. The original drawing is curated in the Collection Lesueur, Muséum d'Histoire Naturelle, Le Havre, France (catalog number 76006). **Below**, ink drawing by Lori Grove of a specimen (MCZ 54265, 405 mm SL) from the Connecticut River in western Massachusetts, the source population for most specimens examined in this study.

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Eric J. Hilton, Lance Grande, and William E. Bemis

Abstract

Sturgeons of the family Acipenseridae comprise 25 extant species, making it the most species-rich extant family of basal (i.e., nonteleostean) actinopterygians. Because of their basal position within Actinopterygii, the anatomical study of sturgeons has a long and rich history, although there remains much to be discovered. Here we describe and illustrate the skeletal anatomy of the shortnose sturgeon, *Acipenser brevirostrum*, as a representative of the family Acipenseridae. *Acipenser brevirostrum*, which is distributed along the east coast of North America, is a relatively small species of sturgeon, reaching a maximum of just over 1 m in total length. Our study is based on 105 skeletal and 147 alcohol-stored specimens representing a broad range of ontogenetic stages (ca. 18 to 1000+ mm TL). This study emphasizes the bony portions of the skeleton, their ontogeny, and parts of the skeleton that persist as cartilaginous elements into the adult stage; the earliest stages of development of the chondrocranium, however, will be the subject of a future project. In the present study, we intend to provide baseline data for future comprehensive ontogenetic and morphological studies of Acipenseridae. Although the Acipenseriformes are extremely morphologically derived compared to most basal actinopterygians, these data will be useful in broader systematics studies of basal Actinopterygii generally. Based on previous studies of acipenseriform phylogeny and using new anatomical data collected in this study, we studied the phylogenetic relationships of fossil and living acipenserids. The monophyly of Acipenseriformes is supported by two synapomorphies: palatoquadrates with symphysis between *pars autopalatina* and the absence of premaxillae and maxillae. Contrary to other recent studies, we recover †*Chondrosteus* as most basal among Acipenseriformes rather than †*Peipiaosteus*. †*Peipiaosteus* + Acipenseroidei is supported by the presence of fewer than seven but more than one branchiostegals, the posterior margin of the branchiostegals serrated, the absence of ossified basibranchials, and the absence of teeth on the gill rakers. Acipenseroidei (= Polyodontidae + Acipenseridae) is supported by one synapomorphy (presence of ventral rostral bones). Monophyly of both Polyodontidae and Acipenseridae is well supported. The family Polyodontidae (represented in our analysis by †*Protopsephurus* and *Polyodon*) is supported by the presence of well-developed anterior and posterior divisions of the *fenestra longitudinalis*, the parietals extending posterior to posttemporals, the presence of stellate bones, the ascending process of parasphenoid extending perpendicularly from the lateral margin of the parasphenoid, a serrated posterior margin on the subopercle, and the presence of "microctenoid" scales. The family Acipenseridae is supported by 11 synapomorphies: arching of the rostral canal, a single posteriormost ventral rostral bone, branchiostegals of different shapes, dorsalmost branchiostegal pillar-like and laterally concave, the presence of the palatal complex, an anterior shelf of hypobranchial one, a continuous series of median dorsal scutes extending from skull to dorsal fin, the supracleithrum reaching the level of extrascapulars, a cardiac shield formed by shoulder girdle, the clavicle–cleithrum suture tight and interdigitating, and the presence of a supracleithral cartilage. Within Acipenseridae, we recovered three groupings; *Acipenser* is not monophyletic. Within Acipenseridae, two supraspecific taxonomic groups are recognized and defined: Husinae (new usage) includes *A. ruthenus* and *Huso huso*, and Pseudoscaphirynchinae new subfamily includes *A. stellatus* and *Pseudoscaphirhynchus*. Husinae is defined by the frontal bones meeting in midline and a slight medial dermopalatine expansion, although neither of these characters is unique to this clade. *Acipenser baerii* is more closely related to Husinae than other acipenserids based on the presence of a variable number of distinctly raised prominences on the ventral rostral bones but is excluded from the subfamily pending further study, including denser taxon sampling within *Acipenser*. The new subfamily Pseudoscaphirynchinae is defined by having the horizontal arm of jugal bone undercut the nasal capsule, a uniquely derived character. Although suitable specimens of all species of Acipenseridae were not available, we note that this is the first robust morphological phylogenetic study addressing species-level relationships for this family, and we hope our study will serve as a baseline study for future comparative anatomical and systematic studies of Acipenseridae.

Introduction

So long as one does not, during analysis, lose sight of the animal as a whole, then beauty increases with increasing awareness of detail.

—Niko Tinbergen, *Curious Naturalists* (1958, p. 144)

General Background and Purpose of Study

In the introduction to the final volume of the *Catalogue of Fishes of the British Museum*, Albert E. Günther (1870, pp. ix–x) wrote of fishes, "No other class of the vertebrates is of equal importance to the geologist and palaeontologist." Within this singular group, sturgeons of the family Acipenseridae are of great phylogenetic significance. With four extant genera and 25 currently recognized living species (Nelson, 2006), Acipenseridae has the most species of any extant family of basal (i.e., nonteleostean) actinopterygian fishes, and its members are often regarded as "living fossils" (Gardiner, 1984). Basal actinopterygians are roughly equivalent to those organisms also referred to as "lower actinopterygians" in the literature. However, it is important to note Theodore Gill's (1872, p. xxxvi) strongly worded caution about the use of "higher" and "lower" when referring to taxa and the unintended *Scala natura* baggage these terms convey: "Perhaps there are no words in science that have been productive of more mischief and more retarded the progress of biological taxonomy than those words, pregnant with confusion, High and Low, and it were to be wished that they might be erased from scientific terminology." There are over 250 genera of nonneopterygian fishes, of which only eight are extant (Gardiner, 1993). In addition to the four extant genera of the Acipenseridae, there are two extant genera of paddlefishes (Polyodontidae) and two extant genera of the Polypteridae.

The Acipenseridae, together with the paddlefishes (Polyodontidae, two extant species, although the Chinese Paddlefish, *Psephurus gladius*, has quite possibly gone extinct recently, as it has not been encountered since 2003; Fan et al., 2006; Turvey et al., 2007; Zhu et al., 2008) and two families known only as fossils (†Chondrosteidae, two species; and †Peipiaosteidae, four species), forms the Acipenseriformes (see Bemis et al., 1997; Jin, 1999). Acipenseriformes are the only living representatives of Chondrostei (*sensu* Grande & Bemis, 1996), which has been interpreted as the living sister group to Neopterygii (gars, bowfins, and teleosts) by most recent researchers (e.g., Patterson, 1982; Gardiner & Schaeffer, 1989; Bemis et al., 1997; Gardiner et al., 2005). The past 20 years have witnessed a flurry of research on sturgeon biology, largely in response to the growing concern of the conservation status of Acipenseriformes (see, e.g., Birstein, 1993; Waldman, 1995). Much of this research has focused on ecology and behavior (e.g., Kynard et al., 2000, 2002a,b, 2003; Zhuang et al., 2003; see also papers in Binkowski & Doroshov, 1985; Holčik, 1989; Birstein et al., 1997c), karyological evolution (e.g., Birstein & Vasiliev, 1987; Birstein et al., 1997a; Fontana et al., 2001), and genetic identification of sturgeon specimens and caviar (e.g., Birstein et al., 1998a,b). All extant species of Acipenseriformes are listed in either Appendix I or Appendix II of CITES, and most are afforded some form of protection in their native ranges, many as "endangered" or "threatened" species.

Sturgeons are easily recognizable fishes, in part because of the unique presence of five rows of bony scutes that run the length of the body and an elongate snout that is ventrally flattened and supports four chemosensory barbels. The caudal fin is strongly heterocercal, and the upper lobe is flanked by rhomboidal scales, a condition found in many nonneopterygian actinopterygians (Smith, 1956; Hilton, 2004; Hilton et al., 2004). To our knowledge, only a single dichotomous key exists for all acipenserid species (P. Vescei's CITES Identification Guide—Sturgeons and Paddlefishes; available at http://www.cws-scf.ec.gc.ca/enforce/pdf/Sturgeon/CITES_Sturgeons_Guide.pdf; site visited July 2009). Many species of Acipenseridae are difficult to distinguish anatomically (e.g., Birstein & Bemis, 1997a), and members of the family are extremely morphologically conservative, in part because of factors such as natural hybridization between taxa (e.g., *A. gueldenstaedtii* and *Huso huso*; Birstein et al., 1997a), high levels of individual morphological variation within taxa (e.g., *A. brevirostrum*; Hilton & Bemis, 1999), and poorly differentiated morphology (e.g., *Scaphirhynchus suttkusi* and *S. platorhynchus*; Mayden & Kuhajda, 1996; Simons et al., 2001).

Several molecular phylogenies of the family Acipenseridae have been presented recently (e.g., Birstein et al., 1997a; Birstein & DeSalle, 1998; Krieger et al., 2000; Ludwig et al., 2000, 2001; Zhang et al., 2000; Fontana et al., 2001; Birstein et al., 2002; Dillman et al., 2007; Peng et al., 2007; Krieger et al., 2008), and there is substantial conflict among the results of these studies. Similarly, there are also significant conflicts between the results of molecular and morphological analyses. Modern morphological analyses of relationships within the family, however, are few and are of varying taxonomic and morphological detail (e.g., Artyukhin, 1995, 2006; Mayden & Kuhajda, 1996; Findeis, 1997, Vasil'eva, 1999, 2009), and we still lack basic morphological knowledge of the group as a whole. For example, Findeis (1993) described the osteology of *Scaphirhynchus*; it is the only acipenserid genus to have been treated in as much morphological detail as fossil and living polyodontids (e.g., Grande & Bemis, 1991; Grande et al., 2002). The skeleton of †*Priscosturion*, a fossil acipenserid genus from the Cretaceous of Montana, has been described in more detail than most extant sturgeons (Grande & Hilton, 2006; note that †*Priscosturion* is replacement name for †*Psamnorhynchus*, which is a genus of flatworms; Grande & Hilton, 2009).

Here, we examine, describe, and illustrate the skeletal anatomy of the shortnose sturgeon, *Acipenser brevirostrum* Lesueur, 1818 (Fig. 1). It is our intent to establish an equivalent data set for the osteology of a representative of the genus *Acipenser* as we have for other Acipenseriformes (e.g., Grande & Bemis, 1991; Findeis, 1993; Grande et al., 2002; Grande & Hilton, 2002) and neopterygians (e.g., Grande & Bemis, 1998; Hilton, 2002b; Grande, 2010). Our choice of *A. brevirostrum* for this project was opportunistic. In cooperation with several colleagues, we assembled a large series of specimens of *A. brevirostrum*, representing a broad range of ontogenetic stages and including many mature specimens (e.g., for studying late stage ontogeny). It is challenging to dissect out contributing sources of variation (Grande, 2004) in the comparative anatomy of sturgeons (e.g., Hilton & Bemis, 1999). While it is certainly reasonable to expect a phylogenetic signal in the comparative anatomical data for sturgeons, this signal often seems to be swamped by the extreme individual variation found in many aspects of their anatomy (Hilton & Bemis, 1999, in press). Our approach is to look methodically

FIG. 1. Live specimens of *Acipenser brevirostrum* Lesueur, 1818. (**A**) Specimen on display at Virginia Living Museum, Newport News, Virginia. (**B**) Close-up of head of three-year-old captive-reared juvenile specimen at Conte Anadromous Fish Laboratory, Turners Falls, Massachusetts. (**C**) Specimen on display at Virginia Living Museum, Newport News, Virginia. (**D**) Head of three-year-old captive-reared specimen at Conte Anadromous Fish Laboratory, Turners Falls, Massachusetts, showing gross malformation of skull in which skull roofing bones medial to the nares failed to develop, resulting in a continuous opening between left and right nares (specimen not retained).

at all body regions and to characterize obvious sources of variation (e.g., ontogenetic variation) as a first step toward detecting clear phylogenetic signals. Morphology is difficult and time consuming but has yet to be fully explored for most groups of fishes within a cladistic framework. Thus, following our anatomical descriptions, we present the results of a new phylogenetic analysis of fossil and living sturgeons based on comparative morphological data.

Previous Studies of the Skeleton of Sturgeons

The focused study of the skeleton of sturgeons enjoys a long history and includes works by many prominent figures in the history of comparative anatomy and systematics of vertebrates in general and fishes in particular (e.g., W. K. Parker, G. R. de Beer, E. Jarvik, E. A. Stensiö, and M. Jollie). However, much of the literature on the osteology of sturgeons is scattered and not widely cited and has yet been synthesized to an adequate degree for modern comparative studies. For example, an early paper on the skull of sturgeons by the Russian worker Modeste Kittary (birth and death dates unknown) is particularly noteworthy (Kittary, 1850), as it appears to have been entirely overlooked in all recent works on sturgeon osteology. In this paper, Kittary described the skull of sturgeons from the Caspian Sea (*A. sturio*, *A. nudiventris*, *H. huso*, *A. ruthenus*, and *A. stellatus*). The taxonomic and morphological nomenclature is, of course, outdated, and the textual descriptions are not as detailed as may be desirable. However, the two plates of illustrations included in this paper struck us as remarkably modern in their execution. In one of these plates (his plate 7), in particular, the skull roofs of the five sturgeon species included in the study are shown in dorsal view, and next to each are detailed illustrations of the stable bones of the skull roof exploded, showing the overlapped regions of each bone and their relation to other elements of the skull roof, much like our approach to illustration of cranial osteology (e.g., Grande & Bemis, 1998; Hilton, 2002b; Grande, 2010).

The contributions to the anatomy and systematics of sturgeons made by two other Russian researchers, A. N. Sewertzoff (whose surname is also often transliterated as Severtsov) and L. S. Berg, are also noteworthy. Aleksei Nikolaevich Sewertzoff (1866–1936), a comparative anatomist based in Moscow, made major contributions to the knowledge of the anatomy of sturgeons, particularly the development of the skeleton and muscles (e.g., Sewertzoff, 1926c, 1928), scales and scutes (e.g., Sewertzoff, 1926b), and the pelvic skeleton (e.g., Sewertzoff, 1926a, 1934). Although many of his taxonomic and evolutionary schemes regarding sturgeons (e.g., his placement of Acipenseriformes as the most basal group of extant fishes; Sewertzoff, 1925) have been criticized (e.g., Watson, 1925; Stensiö, 1932) and have been superseded based on cladistic principles (e.g., Patterson, 1982), the empirical results of his morphological studies are lasting.

Among his many important contributions to ichthyology generally (e.g., Berg, 1940a, 1948a), Leo Semenovich Berg (1876–1950) made fundamental studies on the taxonomy and biology of sturgeons. These include a genus-level classification of the family still used today (Berg, 1904), a 50-page treatise on the systematic position of sturgeons within fishes (Berg, 1948b), and identification of winter and vernal "races" of sturgeons in discussion of anadromous fishes generally (e.g., Berg, 1959). Two of his papers (Berg, 1940b, 1948b) challenged Sewertzoff's hypotheses on the relationships of *Polypterus* and sturgeons, respectively. See Birstein and Bemis (1997b) for more on Berg's life and his many contributions to sturgeon biology.

References on Skeletal Anatomy—We list here some key references on the osteology of sturgeons; other references are provided in the main text. Authors are listed in alphabetical order, and references are arranged by the portion or portions of the skeleton that are discussed (i.e., some references are listed twice if a particular publication deals with more than one region of the skeleton). These lists are not meant to be comprehensive, and some references are omitted because they are, for instance, generally comparative and only superficially concern sturgeons. The most comprehensive treatment of the anatomy of sturgeons yet to be published is that of Marinelli and Strenger (1973), who described the complete anatomy (osteology and soft-tissue anatomy) of *A. ruthenus*. Other noteworthy studies concern morphology of the skeleton of particular taxa and include Deng and Hu (1988) for *A. dabryanus* and Findeis (1993) for *S. platorhynchus*.

Dermal Bones of the Skull, Including Bones of Skull Roof, Circumorbital Region, Anamestic Bones of Dorsal Rostrum, Ventral Rostrocranial Skeleton, Opercular Series, Oral Jaws, and Palatoquadrate and Its Ossifications—Allis (1905, 1935); Antoniu-Murgoci (1936a,b,c,d, 1942); Arratia and Schultze (1991); Bugajew (1930); de Beer (1925, 1937); Gregory (1933); Hilton (2002a, 2005); Hilton and Bemis (1999); Holmgren and Stensiö (1936); Jarvik (1948); Jollie (1980); Kittary (1850); Parker (1873, 1882); Pehrson (1944); Sewertzoff (1926c, 1928).

Braincase (= Chondrocranium and Its Ossifications)—de Beer (1925, 1937); Hilton and Bemis (1999); Holmgren and Stensiö (1936); Stensiö (1932).

Visceral Skeleton, Including Hyoid Arch and Gill Arches—de Beer (1925, 1937); Holmgren and Stensiö (1936); Nelson (1969); Sewertzoff (1928); Springer and Johnson (2004).

Postcranial Axial Skeleton, Including the Vertebral Column, Caudal Fin and Supports, Dorsal and Anal Fins and Supports, Scutes, and Scales—Arratia et al. (2001); Bartsch (1988); Gadow and Abbott (1895); Hilton (2004); Hilton and Bemis (1999); Remane (1936); Ryder (1890); Schmalhausen (1913); Sewertzoff (1926b); Smith (1956).

Appendicular Skeleton, Including Pectoral Fin and Girdle and Pelvic Fin and Girdle—Jessen (1972); Jollie (1980); Meissner (1907); Sewertzoff (1926c, 1934).

References on Early Ontogeny—Although our descriptions of skeletal ontogeny include data on early ossification and chondrification patterns of *A. brevirostrum*, we have not included any description of early (i.e., embryological) development in this paper. There are many data available on early development for *Acipenser*, and references that are not cited in this paper in other contexts include the following: Zalensky (1878), Salensky (1881), Ryder (1890), Jungersen (1893), Neumayer (1932), Dettlaff and Ginsburg (1954), Ginsburg and Dettlaff (1955, 1991), Ballard and Ginsburg (1980), Schmalhausen (1991), and Gisbert (1999).

Materials and Methods

Preparation and Study Methods

Our specimens of *A. brevirostrum* make up a near-complete posthatching growth series and included 105 skeletal (14.8 mm TL to 1060 mm SL) and 147 alcohol-stored (9.5 mm TL to 700 mm SL) specimens. Skeletal materials studied consist of both dried and cleared and stained specimens. All new dry skeletons (almost all of those examined) were prepared from fresh (i.e., not formalin-fixed) specimens. The branchial arches, the ventral portions of the hyoid arch, palatoquadrate, and lower jaws were removed as a single unit. Specimens to be prepared by carpet beetles (Dermestidae) were air-dried in a fume hood or dehydrated in alcohol (see Bemis et al., 2004) and placed in a dermestarium. After beetle preparation, remaining tissue was removed by hand. Some skeletal specimens (often portions of otherwise dry skeletons) were further prepared by maceration in water or a warm trypsin solution and stored as disarticulated elements. Some portions of skeletons were cleaned by hand using a "hot water and picking" method (e.g., Hildebrand, 1968) and are stored in alcohol. On dissection of fresh adult specimens, the cartilaginous portions of the skeleton were found to be a deep reddish color, likely the result of lipids in the cartilage or blood that had soaked into cartilages during freezing; cartilages usually turned white after soaking in a weak ammonia solution and storage in alcohol. Several fresh specimens were dissected, and their skeletons were hand cleaned and placed in alcohol; ossifications were stained by adding a solution of alizarin red to the alcohol. Once the bone had stained, the specimens were returned to clean alcohol for storage (see also Hilton & Bemis, 1999). The clearing and staining protocol of whole specimens for study of bone (stained with alizarin red S) and cartilage (stained with alcian blue 8GX) was based on that of Dingerkus and Uhler (1977) as modified by Hanken and Wassersug (1981; see also Wassersug, 1976). Specimens were examined with the aid of Wild M5 or other dissecting microscopes, equipped with fiber-optic illuminators and/or substage illumination. Specimens examined with scanning electron microscopy (SEM) were mounted on stubs and observed directly (i.e., uncoated) using a variable-pressure Zeiss (formerly LEO) EVO 60 XVP scanning electron microscope.

Information and references regarding the taxonomy and synonymy of sturgeons (e.g., that presented in Systematic Descriptions) are drawn primarily from Eschmeyer and Fricke (2008).

Anatomical Directionality

Following standard anatomical practice, terminology regarding directionality (e.g., anterior, posterior, proximal, and distal) is made in reference to an imaginary line passing from the tip of the snout to the point at which the notochord turns dorsally in the ural caudal skeleton, that is, the axis of the body. In most cases, this is unremarkable. However, the organization of some parts of the skeleton of sturgeons differs from those of most actinopterygians (e.g., the mouthparts), thereby resulting in differing application of these terms for certain elements than is typically found in other actinopterygians (for comments regarding a similar issue in the description of dorsal gill arch musculature, see Springer & Johnson, 2004, p. 4). For example, the suspensorium of sturgeons is "shifted" 90 degrees relative to that found in most other actinopterygians (e.g., the quadrate is lateral rather than posterior to the autopalatine). Therefore, the anterior margin of the suspensorium comprises the free margin of the dermopalatine (which forms the lateral margin of the suspensorium of most other actinopterygians). This differs from the use of anterior for the description of the suspensorium in other recent anatomical descriptions of Acipenseriformes (e.g., Grande & Bemis, 1991, 1996; Grande et al., 2002; Grande & Hilton, 2006).

Counts

Counts of serially arranged elements (e.g., scutes) are numbered anterior (anteriormost = one) to posterior. An exception to this is for preural caudal vertebrae, which are numbered with reference to the first vertebral segment to support a hypural (= ural caudal vertebrae 1); for example, the vertebra immediately anterior to that which supports hypural one is preural caudal one (pu1).

Fin rays (lepidotrichia) are recorded as one of three types: 1) rudimentary fin rays (Grande & Bemis, 1998, p. 25) are unsegmented elements that lie in series with the segmented rays (i.e., their proximal ends reach the proximal base of the fin; this distinguishes them from fringing fulcra, the proximal ends of which do not reach the base of the fin) but still are formed by paired elements (i.e., hemitrichia, which distinguishes them from basal fulcra); 2) segmented fin rays (= principal fin rays of Grande & Bemis, 1998, p. 27; this type of ray includes all branched rays) are divided into two or more sections along the longitudinal axis of the fin ray; and 3) branched fin rays are forked distally at least once. For a detailed discussion of the fin-ray elements of osteichthyans, see Arratia (2008, 2009). The definitions of basal and fringing fulcra presented by Arratia in these papers differ slightly from those followed here. In her conception, basal fulcra may also be paired structures but precede the bases of the median fins and may be organized in one of two patterns (her Patterns I and II), depending on the distribution of paired/median elements within a series. She defined fringing fulcra as "paired structures associated with the leading edge of paired and/or unpaired fins" and classified them into three types depending on their distribution, form, and relationship to the leading fin ray(s) (Patterns A–C; Arratia, 2009, p. 227). We do not dispute the diversity of these and other fin elements described and illustrated by Arratia (2008, 2009). However, our definitions reflect recent literature on acipenseriform anatomy and are useful as such.

Scutes of sturgeons are large bony plates usually organized in distinct series. As noted by Hilton (2004, p. 606), the distinction between scutes and basal fulcra is often "blurred and possibly arbitrary when the two [types of structures] are continuous" (e.g., in the dorsal fin of sturgeons; often in the caudal fin of basal actinopterygians). Arratia (2009) noted significant variation in the structure of "scutes" across actinopterygians, and it is likely that the "scutes" of sturgeons are not homologous to "scutes" of other basal actinopterygians (indeed, we suggest below that even the dorsal, lateral, and ventral scutes in sturgeons are not the product of similar developmental or evolutionary origins). However, the term "scute" is widespread, and we see little advantage to changing the terminology until the variation is better understood,

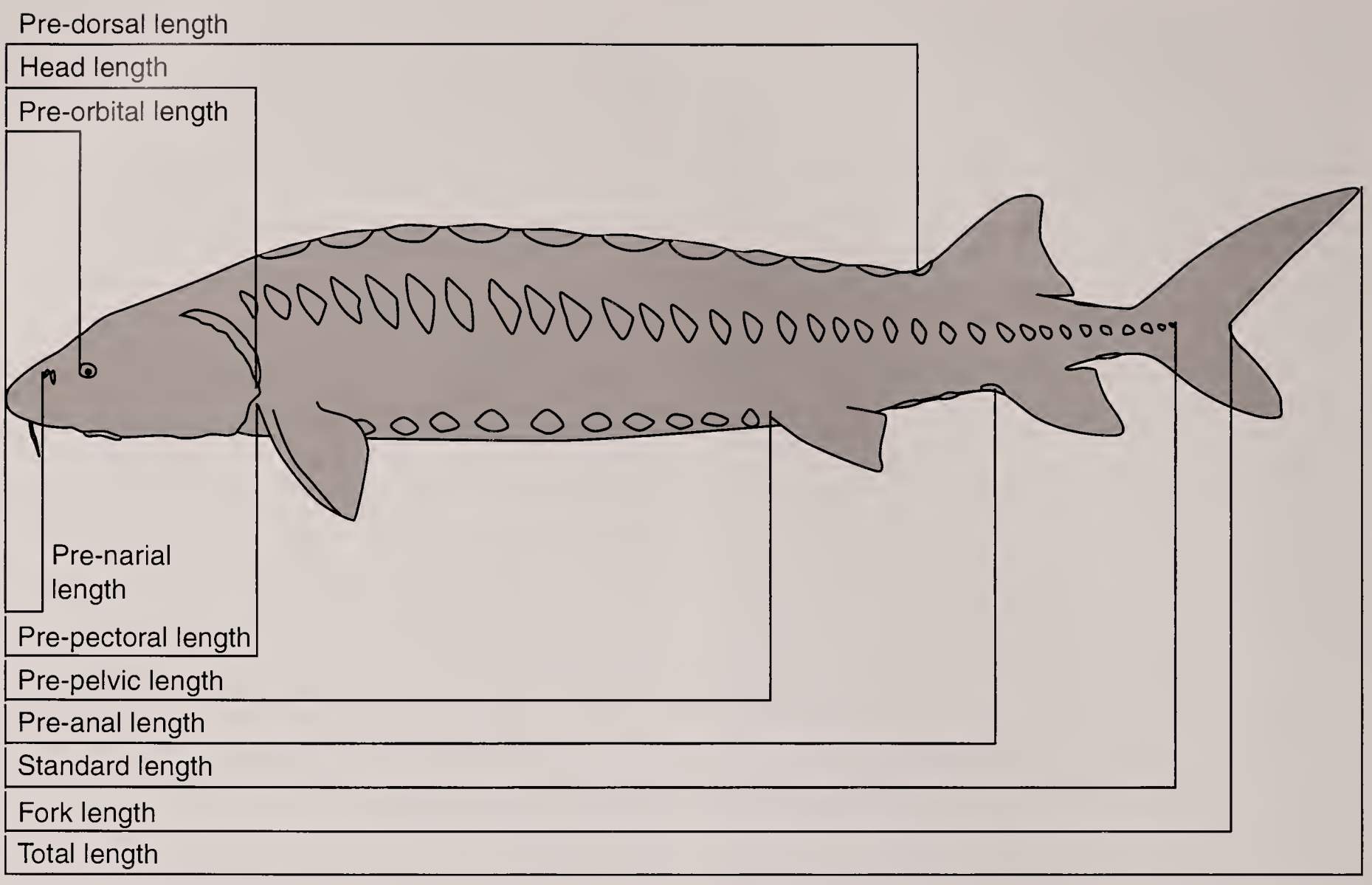


FIG. 2. Measurements of body and head taken for a sample of *Acipenser brevirostrum*; see text for explanation. Modified from Hilton and Bemis (in press).

particularly for the series of bony plates found in sturgeons. In sturgeons, the five primary rows of body scutes include a median dorsal series and paired lateral and ventral series. These scutes are counted as the number of elements in the series. The anteriormost dorsal scute becomes incorporated into the skull roof in the adult and is included in the count of dorsal scutes. Scutes are numbered anterior to posterior (e.g., the anteriormost dorsal scute is dorsal scute 1); no homology between elements is implied by such a numbering system. There are other irregularly arranged series of scutes on the caudal peduncle, but these are highly individually and interspecifically variable in their form, position, and number. The distinction between these irregular scutes and the small dermal platelets found distributed in the skin is admittedly arbitrary and based purely on the relative sizes of the element. Scute-like elements that lie immediately anterior to the dorsal and anal fins were not included in the counts of scutes following the observation of their morphological and developmental distinctness made by Findeis (1993); these elements were termed the dorsal and anal fin fulcra by Hilton (2004), and this terminology is followed here.

Measurements

Body measurements (Fig. 2) follow those of Hilton and Bemis (in press), which derive in part from those of Birstein et al. (1997a). All measurements are taken in a straight line (i.e., not following the curve of the body). Measurements were recorded to the nearest millimeter except for measurements below 35 mm, which were taken with the use of digital calipers and recorded to the nearest 0.1 mm (some of these measurements recorded early in this study were taken to the nearest millimeter). Obviously damaged or anomalous (e.g., due to teratological, pathological, or preservational effects) specimens were excluded for some or all measurements as appropriate.

Total length was measured from the anterior tip of the snout to the posteriormost tip of the caudal fin. When reasonable, this was estimated if the tail of a specimen is noticeably damaged.

Fork length was measured from the anterior tip of the snout to the fork of the caudal fin.

Standard length was measured from the anterior tip of the snout to posteriormost keeled lateral scute.

Prepelvic fin length was measured from the anterior tip of the snout to the anterior base of the pelvic fin.

Prepectoral fin length was measured from the anterior tip of the snout to the anterior base of the pectoral fin.

Predorsal fin length was measured from the anterior tip of the snout to the anterior base of the dorsal fin.

Preanal fin length was measured from the anterior tip of the snout to the anterior base of the anal fin.

Head length was measured from the anterior tip of the snout to the posteriormost extent of the subopercle bone.

Preorbital length was measured from the anterior tip of the snout to the anterior bony margin of the orbit.

Prenarial length was measured from the anterior tip of the snout to the anterior margin of the anterior nares.

Prebarbel length was measured from the anterior tip of the snout to base of the anteriormost barbel.

Preoral length was measured from the anterior tip of the snout to the anterior extent of the upper jaw (the upper "lip") with the mouth fully retracted.

Mouth width was measured as the distance between the left and right corners of the jaws, including the fleshy "lips."

Dentary length was measured as the length of the ossified dentary.

Skull width was measured as the widest part of the skull roof (near the posterior part of the dermopterotics).

Skull length was measured from the anterior tip of the snout to the posterior margin of the first dorsal scute (for small specimens this element was not incorporated into the skull roof).

Exposed parietal length was measured as the maximum anterior–posterior length of the parietal bone exposed on the dorsal surface of the skull roof; both left and right parietals were measured and recorded.

Fin base length was measured as the distance between the anterior and posterior insertion of the fin for all paired (typically left side only) and median fins (except the caudal fin).

Length of dorsal lobe of caudal fin was measured from the anterior base of the dorsal lobe of the caudal fin to its posterior tip.

Length of ventral lobe of caudal fin was measured from the anterior base of the ventral lobe of the caudal fin to its posterior tip.

Photographs and Line Illustrations

All photographs were taken digitally; contrast and color balance of images were adjusted using Adobe Photoshop. All line drawings (except the whole specimen illustrated for the cover and Fig. 97) were rendered electronically using Adobe Illustrator software and were based on the digital images.

Materials Examined

The following is a list of specimens of Acipenseriformes that were examined and/or prepared during the course of this study; specimens of nonacipenseriform taxa are referred to in the text where relevant. Additional specimens listed by Hilton (2002a, 2005) and Hilton et al. (2004) but not listed below were also examined. In this list, the dispositions of specimens are indicated as stored in alcohol (a), serially sectioned (sec), cleared and double stained (cs), or dry skeleton (ds); standard lengths (SL) or total lengths (TL) are provided if known or estimated (est.). A dagger (†) precedes all taxa known only as fossils.

Acipenseridae

Acipenser baerii Brandt, 1869: FMNH 117783 (1 ds, est. 875 mm SL); FMNH 117784 (1 ds, est. 870 mm SL); FMNH 117786 (1 a, est. 800 mm SL); FMNH 117785 (1 ds, est. 810 mm SL); MCZ uncataloged (1 cs; head only; juvenile); VIMS 12083 (1 ds, est. 950 mm TL).

Acipenser brevirostrum Lesueur, 1818: specimens examined are listed in taxonomic description, below (p. 15).

Acipenser dabryanus Duméril, 1869: AMNH 10904 (1 a, 315 mm SL).

Acipenser fulvescens Rafinesque, 1817: FMNH 85157 (1 ds, est. 1,200 mm SL); FMNH 98256 (1 ds, est. 800 mm SL); MCZ 8911 (1 a, 259 mm SL); UMMZ 101624 (1 a, 325 mm SL); UMMZ 101610 (1 a, 380 mm SL); UMMZ 196995 (1 a, est. 480 mm SL); UMMZ 201624 (1 a, 468 mm SL); UMMZ 101619 (1 a, 482 mm SL); UMMZ 97889 (1 a, 500 mm SL); UMMZ 101741 (1 a, 645 mm SL); UMMZ 96915 (1 a, 695 mm SL); UMMZ 97890 (1 a, 755 mm SL); UMMZ 97913 (1 a, 850 mm SL); UMMZ 97895 (1 a, 820 mm SL); UMMZ 97900 (1 a, 1050 mm SL); UMMZ 223764 (1 cs, 185 mm SL; 2 a, 192–206 mm SL).

Acipenser gueldenstaedtii Brandt and Ratzeberg, 1833: ANSP 82443 (1 a, 113 mm SL); BMNH 73.4.21.20 (1 a, 240 mm SL); UMMZ 174596 (1 a, 217 mm SL).

Acipenser medirostris Ayres, 1854: AMNH 46035 (1 ds, unknown SL); AMNH 47760 (1 ds, unknown SL); AMNH 47761 (1 ds, unknown SL); CAS 36968 (2 a, 205–210 mm SL); CAS SU 67675 (3 a, 152–295 mm SL); UMMZ 94428 (1 a, 470 mm SL).

Acipenser mikadoi Hilgendorf, 1892: UMMZ 210695 (1 a, 325 mm SL).

Acipenser nacarii Bonaparte, 1836: ANSP 624 (syntype, 1 a, 245 mm SL); ANSP 625 (syntype, 1 a, 255 mm SL); BMNH 1900.3.29.50 (1 a, 345 mm SL); CAS 19761 (1 a, 395 mm SL).

Acipenser nudiventris Lovetzky, 1828: BMNH 1925.8.6.3 (1 a, 210 mm SL).

Acipenser oxyrinchus Mitchill, 1815: UMMZ 114257 (1 a, 480 mm SL); USNM 94726 (1 ds, large adult, unknown SL); USNM 110207 (1 ds, small adult, unknown SL). In addition, many (>15) fresh and frozen specimens (large juveniles and adults) currently uncataloged at VIMS were examined, dissected, and/or prepared as skeletons.

Acipenser ruthenus Linnaeus, 1758: AMNH 1554 (1 ds, est. 300 mm SL); CAS SU 20584 (1 a, 240 mm SL); MCZ 25552 (2 a, 188–203 mm SL); UMA F10369 (3 cs, unknown SL, heads only, small juveniles); UMMZ 174595 (2 a, 245–255 mm SL); USNM 10195 (1 a, 420 mm SL).

Acipenser schrenckii Brandt, 1869: BMNH 79.11.14.56 (1 a, 275 mm SL); MCZ 32345 (2 a, 178–206 mm SL).

Acipenser sinensis Gray, 1834: AMNH 17736 (1 a, 342 mm SL); CAS 217165 (1 a, 397 mm SL).

Acipenser stellatus Pallas, 1771: BMNH 64.4.25.48 (1 a, 510 mm SL); MCZ uncataloged (1 cs, length unknown, head only, juvenile); UMMZ 145831 (1 a, 223 mm SL); UMMZ 174597 (1 a, 225 mm SL); UMMZ 184979 (3 a, 175–190 mm SL); UMMZ 184980 (1 cs, 160 mm SL; 2 a, 84–112 mm SL).

Acipenser sturio Linnaeus, 1758: AMNH 215830 (1 ds, est. 350 mm SL); CAS SU 21254 (1 a, 161 mm SL); MCZ 23441 (1 a, 318 mm SL); USNM 143251 (1 a, 272 mm SL).

Acipenser transmontanus Richardson, 1836: AMNH 46033 (1 ds, unknown SL); AMNH 46034 (1 ds, unknown SL); AMNH 47755 (1 ds, unknown SL); CAS 30268 (1 a, 355 mm SL); FMNH 117777 (1 ds, unknown SL, 340 mm head length); FMNH 117778 (1 ds, unknown SL, 340 mm head length); FMNH 117779 (1 ds, unknown SL, 300 mm head length); FMNH 117780 (1 a, unknown SL, 295 mm head length); FMNH 117781 (1 ds, unknown SL, 385 mm head length); FMNH 117782 (1 ds, unknown SL, 350 mm head length); UMMZ 94427 (1 a, 510 mm SL); UMMZ 94426 (1 a, 655 mm SL); UMMZ 94426 (1 a, 720 mm SL); VIMS 12097 (1 ds, est. 580 mm SL).

Huso dauricus (Georgi, 1775): BMNH 1910.1.7.1-2 (2 a, est. 430–est. 530 mm SL); BMNH 1925.8.6.2 (1 a, 225 mm SL); MCZ 32343 (1 a, 252 mm SL).

Huso huso (Linnaeus, 1758): AMNH 1553 (1 ds, est. 300 mm SL); ANSP 82495 (3 a, 88–106 mm SL); CAS 211810 (1 cs, 130 mm SL); FMNH 76853 (1 a, est. 830 mm SL); FMNH 1 a, est. 820 mm SL); FMNH uncataloged (1 a, est. 875 mm SL); MCZ 54269 (1 a, 228 mm SL; CT scanned).

†*Protoscaphirhynchus squamosus* Wilimovsky, 1956: UMMP 22210 (portions of skull, body, and caudal fin; length unknown; see Hilton & Grande, 2006).

Pseudoscaphirhynchus kaufmanni (Bogdanov, 1874): AMNH 97566 (1 cs, 350 mm TL; measurement from Findeis, 1993, as specimen disarticulated during clearing and staining), INHS 64426 (1 a, 162 mm SL); UAIC 13265.01 (1 a, 188 mm SL; CT scanned).

Pseudoscaphirhynchus hermanni (Sewertzoff in Kessler, 1877): UAIC 13252.01 (1 a, 171 mm SL). Also, three uncataloged cleared and stained specimens were examined (168–183 mm SL), representing three forms of this species.

†*Priscosturion longipinnis* (Grande & Hilton, 2006): MOR 1184 (holotype; whole specimen, est. 800 mm TL); TMP 90.104.6 (crushed head and pectoral girdle; TL unknown, but an individual substantially larger than MOR 1184); = †*Psammorhynchus longipinnis* (see Grande & Hilton, 2009).

Scaphirhynchus platorynchus (Rafinesque, 1820): FMNH 10324 (1 ds, unknown SL); FMNH 45024 (1 of 2 a, 290 mm SL, CT scanned); FMNH 98286 (1 ds, unknown SL); VIMS 12098 (1 cs, 250 mm SL).

†Chondrosteidae

†*Chondrosteus acipenseroides* Egerton, 1858: FMNH P25090 (isolated caudal fin); specimens listed in Hilton and Forey (2009), which includes all specimens in BGS, BMNH, and UMO.

†Peipiaosteidae

†*Peipiaosteus pani* Liu and Zhou, 1965: FMNH PF14371 (whole fish, est. 320 mm TL), FMNH PF14370 (whole fish, 184 mm TL); see Grande and Bemis (1996).

Polyodontidae

†*Crossopholis magnicaudatus* Cope, 1883: FMNH PF11896A, B (large juvenile or adult; unknown TL); FMNH PF13550B (adult, unknown TL); FMNH PF11898 (est. 900 mm TL).

Polyodon spathula (Walbaum, 1792): AMNH 218237 (1 ds, unknown TL, adult), FMNH 98245 (1 ds, 800 mm TL), FMNH 98247 (1 ds, 1,020+ mm TL), FMNH 98287 (1 ds, unknown TL, skull length = 330 mm), UMA F10525 (1 ds, unknown TL, skull length = 470 mm), UMA uncatalogued (1 ds, tail only; unknown TL).

Psephurus gladius (Martens, 1862): FMNH 99131 (1 cs; 200 mm TL); USNM 117477 (1 cs, 890 mm TL).

†*Protopsephurus liui* Lu, 1994: specimens listed in Grande et al. (2002).

List of Abbreviations

Anatomical Abbreviations

In general, names of bones and cartilages follow those of Grande and Bemis (1998) where applicable; exceptions are noted in the text. Where applicable, following our name for an element, we list a synonymy of names drawn from other descriptions of acipenserid osteology (e.g., Parker, 1882; Sewertzoff, 1926c; Jollie, 1980; Findeis, 1993). For detailed discussion of the terminology of actinopterygian cranial and postcranial skeletal elements, see Schultze (2008) and Arratia (2008, 2009), respectively. Below is a partially annotated list of the abbreviations used in the figures and text.

abf, basal fulcrum associated with anal fin; **af**, anal fin; **amo**, developing ampullary organs; **an**, aortic notch of parasphenoid; **aoc**, aortic canal; **ap**, autopalatine; **ar**, articular; **arp**, ascending ramus of the parasphenoid; **bbc**, basibranchial copula; **bd**, basidorsal; **be**, basipterygial elements of the pelvic girdle (= proximal pelvic radials); **br**, branchiostegal (= subopercle and interopercle of Sewertzoff, 1926c); **brb**, border rostral bones; **btp**, basitrabecular processes of the neurocranium; **bv**, basiventral; **cb**, ceratobranchial; **cf**, caudal fin; **cha**, anterior ceratohyal; **chp**, posterior ceratohyal; **cl**, cleithrum; **clv**, clavicle; **cor**, coracoid; **ctp**, central trabecular process of the neurocranium; **d**, dentary; **daf**, dorsal rostral ampullary field; **dbf**, dorsal fin basal fulcrum; **dcf**, dorsal caudal fulcra; **df**, dorsal fin; **dpl**, dermopalatine (= maxilla of Jollie, 1980); **dplt**, dermopalatine teeth; **dpp**, dorsal process on the pelvic girdle; **dpt(v)**, ventral lamella of the dermopterotic; **dpt**, dermopterotic (= squamosal of Sewertzoff, 1926c; dermosphenopterotic of Allis, 1935; intertemporo–supratemporal of Jollie, 1980); **dr**, distal radial; **drb**, dorsal rostral bones; **ds1**, first dorsal scute (= postoccipitale of Sewertzoff, 1926c; median nuchal of Jollie, 1980); **dsp**, dermosphenotic (= supraorbital of Sewertzoff, 1926c; Gregory, 1933; Allis, 1935); **dt**, dentary teeth; **eb**, epibranchial; **ecp**, ectopterygoid; **ecpt**, ectopterygoid process of the palatopterygoid; **ehc**, external hyomandibular cartilage; **ehyc**, external hyoid arch cartilage; **epbr**, epiphyseal bridge; **epo**, epioccipital; **excl**, lateral extrascapular; **excm**, median extrascapular (= dermosupraoccipitale of Sewertzoff, 1926c); **exo**, exoccipital; **f?**, unidentified foramen; **fca**, foramina for caudal arteries; **feba**, foramina in parasphenoid for efferent branchial arteries (Findeis, 1993); **fII**, foramen for the second cranial nerve; **fIII**, foramen for the third cranial nerve; **fIV**, foramen for the fourth cranial nerve; **fIX**, foramen for the ninth cranial nerve; **fot**, foramen for the otic ramus of the facial nerve; **foph**, foramen for the superficial ophthalmic ramus of the anterodorsal lateral line nerve; **fr**, frontal (= parietal of some authors based on its homology with the bone termed the "parietal" in sarcopterygians; e.g., see Jollie, 1986, Arratia & Cloutier, 1996; Schultze 2008; we follow the more commonly used term for this bone in actinopterygian studies); **fra**, unornamented anterior portion of the frontal that lies ventral to anamestic rostral bones; **fsn**, foramina for the spino-occipital nerves; **fsr**, foramen for the spiracular ramus of the otic lateral line nerve; **fV+VII**, foramen for the combined fifth and seventh cranial nerves; **fX**, foramen for the tenth (vagus) cranial nerve; **gcb4**, groove on dorsal surface of proximal end of ceratobranchial 4; **gr**, gill rakers; **h**, hyomandibula; **ha**, haemal arch; **hb**, hypobranchial; **hb1tp**, tooth plates associated with hypobranchial 1, may be supported in the midline by the anterior basibranchial copula; **hh**, hypohyal; **hs**, haemal spine; **hyf**, facet for the hyomandibula; **hyp**, hypural; **ib**, inner barbel; **iclv**, interclavicle; **id**, interdorsal; **ida**, anterior interdorsal; **idp**, posterior interdorsal; **ihy**, interhyal; **iocn**, infraorbital sensory canal; **ipb**, infrapharyngobranchial; **iso**, ossicles between lateral scutes; **iv**, interventral; **j**, jugal (= suborbital of Sewertzoff, 1926c; = ventral postorbital of Jollie, 1980); **lep**, lateral ethmoid process of the neurocranium; **let**, lateral ethmoid; **llcn**, lateral line sensory canal; **llf**, opening of the lateral line (may be on edges of bones and not necessarily visible in drawings); **lrb**, lateral rostral canal bone (= antorbital of Allis, 1905, and others; see Hilton, 2002a); **m**, mentomeckelian; **maf**, middle ampullary field; **map**, median anterior process of the parasphenoid (= subrostral of Sewertzoff, 1926c); **mcor**, mesocoracoid; **mfj**, medial flange of the jugal; **mpec**, ectopterygoid process of the dermopalatine; **mr**, middle radial of the dorsal or anal fin (the middle element of a pterygiophore); **mtg**, metapterygium; **n(t)**, tubular bone anterior of the nasal (= "bar separating the anterior olfactory opening from the posterior one" of Sewertzoff, 1926c); **n**, nasal; **na**, neural arch; **nc**, notochordal sheath; **ncap**, nasal capsule of the neurocranium; **noa**, anterior nasal opening; **nop**, posterior nasal opening; **oaf**, occipital ampullary field; **ob**, outer barbel; **oc**, cartilage of the occipital region of the neurocranium; **ocn**, occipital sensory canal (= supratemporal commissural canal; see Grande & Bemis, 1998); **opaf**, opercular ampullary field; **opo**, opisthotic; **ors**, orbitosphenoid; **os**, orbital shelf; **pa**, parietal (= postparietal of some authors based on its homology with the bone termed the "postparietal" in sarcopterygians; see also comments for frontal); **paa**, unornamented anterior portion of the parietal that lies ventral to anamestic rostral bones; **pap**, unornamented posterior portion of the parietal; **par**, prearticular (= splenial of Starks, 1916); **pas**, parasphenoid; **past**, parasphenoid tooth patch; **pat**, *pars autopalatina*; **pb**, pelvic bone; **pcf**, pectoral fin; **pcl**, postcleithrum; **pfs**, pectoral fin spine; **pg**, groove on the parasphenoid marking the articulation point with the branchial arches; **phy**, parhypural; **plc**, palatal

complex; **pnw**, posterior nasal wall; **po**, postorbital (= postfrontal of Sewertzoff, 1926c; = suprapostorbital of Allis, 1935; = dorsal postorbital of Jollie, 1980); **poaf**, postorbital ampullary field; **pp**, parapophyses; **ppt**, palatopterygoid (= endopterygoid of other authors; e.g., Findeis, 1997; Arratia & Schultze, 1991; although this bone is likely homologous to the endopterygoid of other actinopterygians, we follow the terminology of Grande & Bemis, 1991, 1996, and Grande et al., 2002 for consistency with our other publications on acipenseriform osteology); **pptt**, palatopterygoid teeth; **pq**, *pars quadrata*; **pr**, proximal radial of the dorsal or anal fin (the proximalmost element of a pterygiophore); **prd**, distal pelvic radial; **prm**, middle pelvic radial; **pro**, prootic; **pt(v)**, ventral lamella of the posttemporal; **pt**, posttemporal (= supratemporal of Sewertzoff, 1926c; = lateral extrascapular of Allis, 1935); **ptf**, posttemporal fossa; **ptg**, propterygium; **ptp**, posttemporal process of the neurocranium; **q**, quadrate; **qj**, quadratojugal; **r**, rib; **ra**, radials; **rcb**, rostral canal bones; **rcn**, rostral sensory canal (= lateral basirostrals of Sewertzoff, 1926); **rcs**, rhomboid caudal scales; **s**, spiracle; **sc**, scapula; **scap**, sclerotic capsule; **scc**, scapulocoracoid cartilage; **scl**, supracleithrum (= suprascapular of Allis, 1935); **scla**, anterior opening of the lateral line sensory canal in the supracleithrum; **sclb**, posterior opening of the lateral line sensory canal in the supracleithrum; **sn**, supraneural; **snf**; foramina for spinooccipital nerves; **so**, supraorbital (= prefrontal of Sewertzoff, 1926c; preorbital of Allis, 1935; antorbital of Findeis, 1997); **soaf**, supraorbital ampullary field; **socn**, supraorbital sensory canal; **sop**, subopercle (= opercle of Sewertzoff, 1926c; we follow Tatarko, 1936, and others in interpreting the large gill cover bone as representing the subopercle of other actinopterygians); **spb**, suprapharyngobranchial; **spc**, spinal canal; **sscc**, suprascapulocoracoid cartilage; **stcn**, supratemporal sensory canal; **suaf**, suborbital ampullary field; **tfc**, trigeminofacialis chamber; **uga**, unidentified gill arch element; **vaf**, ventral rostral ampullary field; **vcf**, ventral caudal fulcrum; **vhb**, ventral hyomandibular cartilaginous blade; **vrb**, ventral rostral bone (= medial basirostral of Sewertzoff, 1926c).

Institutional Abbreviations

AMNH, American Museum of Natural History (New York, NY); **ANSP**, Academy of Natural Sciences of Philadelphia (Philadelphia, PA); **BGS**, British Geological Survey (Keyworth, Nottinghamshire, England); **BMNH**, Natural History Museum (London, England); **CAS**, California Academy of Sciences (San Francisco, CA); **FMNH**, Field Museum of Natural History (Chicago, IL); **INHS**, Illinois Natural History Survey (Champaign, IL); **MCZ**, Museum of Comparative Zoology at Harvard University (Cambridge, MA); **MOR**, Museum of the Rockies (Bozeman, Montana); **TMP**, Royal Tyrrell Museum of Paleontology (Drumheller, Alberta, Canada); **UAIC**, University of Alabama Ichthyology Collection (Tuscaloosa, AL); **UMA**, University of Massachusetts Amherst Museum of Natural History (Amherst, MA); **UMMP**, University of Michigan Museum of Paleontology (Ann Arbor, MI); **UMMZ**, University of Michigan Museum of Zoology (Ann Arbor, MI); **UMO**, Oxford University Museum of Natural History (Oxford, England); **USNM**, United States National Museum of Natural History, Smithsonian Institution (Washington, DC); **VIMS**, Virginia Institute of Marine Science (Gloucester Point, VA).

Zoological science is never advanced by general works compiled mechanically and without critical discernment.

—Albert E. Günther (1870, p. xi)

Systematic Descriptions

Osteichthyes Huxley, 1880
Actinopterygii Cope, 1887
Actinopteri Cope, 1871b
Chondrostei Müller, 1844
Acipenseriformes Berg, 1940a
Acipenseridae Bonaparte, 1831

***Acipenser* Linnaeus, 1758, p. 237**

Rejected Synonyms—*Accipenser* Goüan, 1770; *Acipenses* Linck, 1790; *Acipenseres* Heckel and Kner, 1858.

Type Species—*Acipenser sturio* Linnaeus, 1758: 237.

Species Included as Valid—*Acipenser baerii* Brandt, 1869; *A. brevirostrum* Lesueur, 1818; *A. dabryanus* Duméril, 1869; *A. fulvescens* Rafinesque, 1817; *A. gueldenstaedtii* Brandt and Ratzeberg, 1833; *A. medirostris* Ayres, 1854; *A. mikadoi* Hilgendorf, 1892; *A. naccarii* Bonaparte, 1836; *A. nudiventris* Lovetzky, 1828; *A. oxyrinchus* Mitchill, 1815; *A. persicus* Borodin, 1897; *A. ruthenus* Linnaeus, 1758; *A. schrenckii* Brandt, 1869; *A. sinensis* Gray, 1834; *A. stellatus* Pallas, 1771; *A. sturio* Linnaeus, 1758; *A. transmontanus* Richardson, 1836. See Birstein and Bemis (1997a).

Distribution—Fossil and living sturgeons of the genus *Acipenser* are strictly holarctic, distributed in the freshwaters and nearshore marine environments of North America, Europe, and Asia. *Acipenser oxyrinchus* occasionally is found as far south as the coast of French Guiana but is regarded as an accidental from the northern coast of South America (Robins et al., 1986).

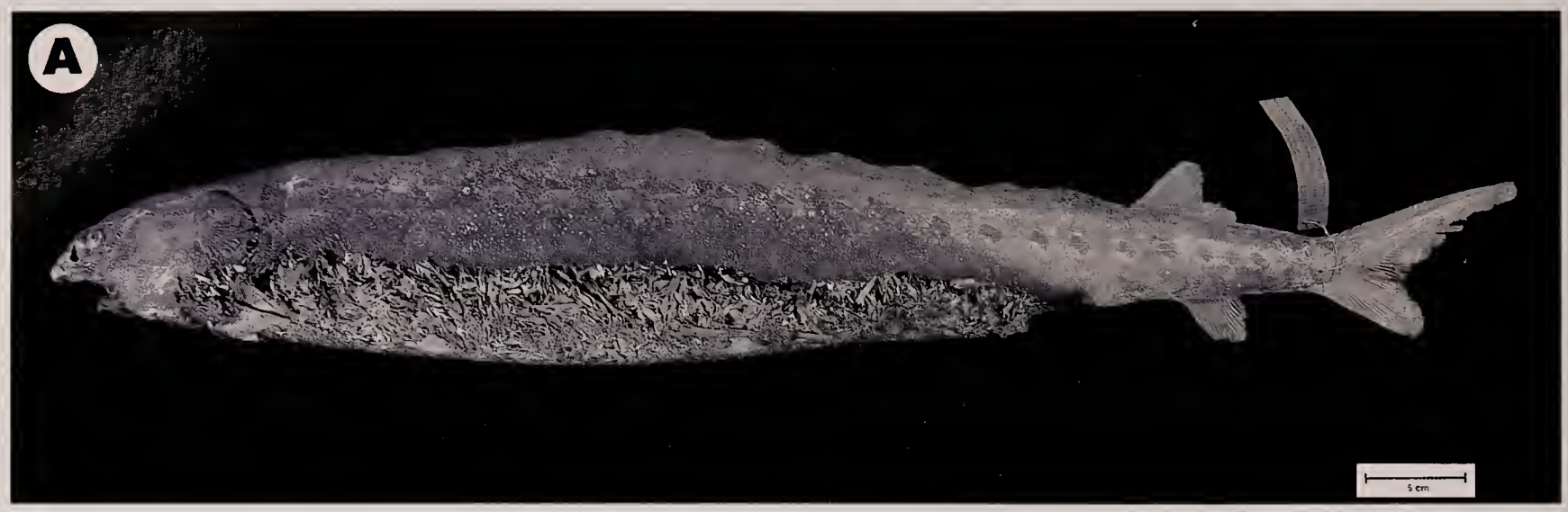
Generic Diagnosis—See Remarks.

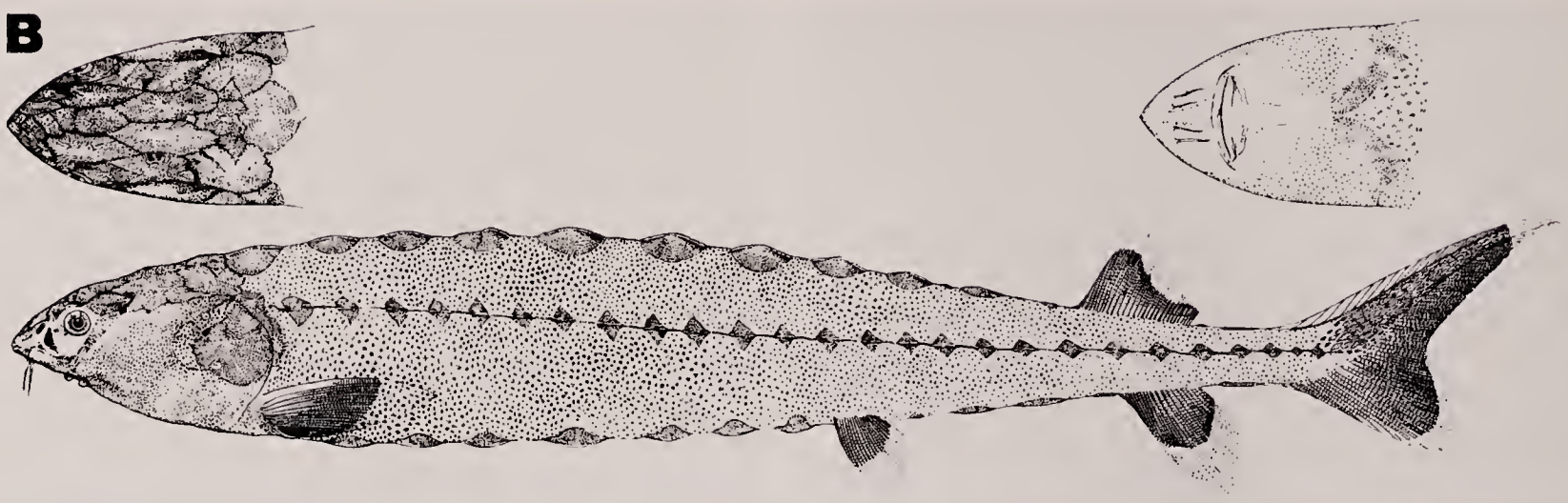
Etymology—*Acipenser*, Latin, the sturgeon. Jaeger (1978, p. 5) noted, "perhaps < *aci-* (< Gr. *okys*), swift + *penna* = *pinna* = OL [Old Latin].*pensa*, a wing, fin." Beebe (1906, p. 261) traced the vernacular term sturgeon to be "from the Saxon word *stiriga*, literally a stirrer, from the habit of the fish of stirring up the mud at the bottom of the water."

Remarks—At this time, we are unable to differentially diagnose the genus *Acipenser*. The results of our phylogenetic study (see pp. 108, Figs. 128, 129) suggest that the genus *Acipenser*, as currently conceived, is paraphyletic. Similar results from molecular analyses (e.g., Birstein et al., 2002; Dillman et al., 2007; Krieger et al., 2008) support this finding. However, we are reluctant to change the genus-level classification of sturgeons until all species can be adequately surveyed from both morphological and molecular perspectives and differential diagnoses can be firmly established.

Linnaeus's (1758, p. 237) original diagnosis of the genus *Acipenser*, which was classified in his "Nantes" group of Amphibia, reads as follows: "*Spiracula* lateralia solitaria, linearia. *Os* sub capite, retractile, edentulum. *Cirri* sub rostro, ante os"; this diagnosis was repeated verbatim in the twelfth edition of *Systema Naturae* (Linnaeus, 1766, p. 403). Beyond *A. sturio*, Linneaus also named *A. ruthenus* and *A. huso* (= *Huso huso*) in the tenth edition (a fourth taxon, "*A. plecostomus*" [= *Plecostomus plecostomus*] was also included in *Acipenser*, although this was changed by the twelfth edition).

Also, as a note, Edward Drinker Cope (1840–1897) first used the group name Actinopteri in the essay "On the systematic relations of the fishes" published in September 1871 in the *American Naturalist* (Cope, 1871b). This essay also appeared as the introductory part of the paper titled "Contribution to the ichthyology of the Lesser Antilles," which was published in December of the same year (Cope, 1871a). Therefore, it is the *American Naturalist* paper that has priority as the source of the name Actinopteri (cf. Patterson, 1982). A more complete explanation of Cope's ideas on the systematics of fishes was published in an article (Cope, 1872) of the same title as Cope (1871b). The months of publication cited here were taken from the annotated bibliography of Cope published by Osborn (1931).





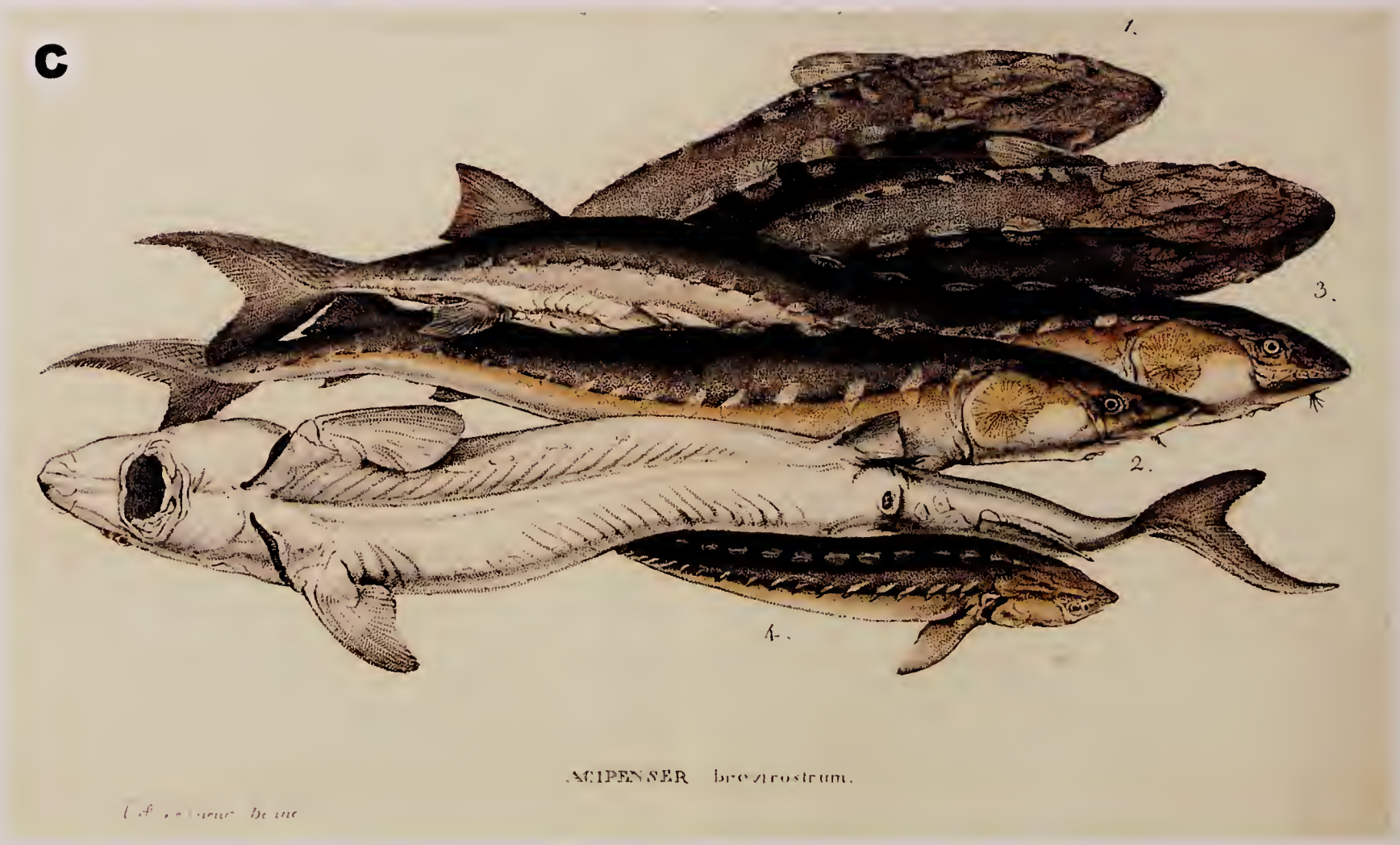


FIG. 3. Holotype of *Acipenser brevirostrum* Lesueur, 1818 (ANSP 16953). (**A**) Lateral view. (**B**) Fowler's (1911) illustration of the holotype in dorsal (head only, left), ventral (head only, right), and lateral views (whole body). Anterior to left. (**C**) Illustration by C. A. Lesueur, published in Lesueur (1827, pl. 7), photo from the copy in the Collection Lesueur, Muséum d'Histoire Naturelle, Le Havre, France (catalog number 76605).

FIG. 4. Map of a portion of the east coast of North America showing distribution of the shortnose sturgeon, *Acipenser brevirostrum*. Range highlighted in blue; type locality (Delaware River; exact collection locality unknown; see Lesueur, 1818) is indicated by a white star.

***Acipenser brevirostrum* Lesueur, 1818, p. 390**
Figs. 1, 3, 5–110.

REJECTED SYNONYMS—*A. brevirostris* Richardson, 1836, p. 278; *A. marginatus* (?) Rafinesque, 1820, p. 79; *A. obtusirostris* Lovetzky, 1834, p. 257; *A. measius* Lesueur, in De Kay, 1842, p. vii (name only); *A. microrhynchus* Duméril, 1870, p. 164; *A. lesueurii* Valenciennes in Duméril, 1870, p. 166; *A. dekayi* Duméril, 1870, p. 168; *A. rostellum* Duméril 1870, p. 173; *A. sinus* Valenciennes, in Duméril, 1870, p. 175; *A. measus* Lesueur, in Vaillant, 1896, p. 26.

HOLOTYPE—A dried, stuffed specimen in poor condition (ANSP 16953; 690 mm SL; Fig. 3A). All internal skeletal elements and soft tissues are missing from this specimen, as are the skin of the ventral surface of the body, most of the ventral scutes from both sides (although a few of each side are still held in place by the stuffing), most of the right pectoral fin, all of the left pectoral fin, and both pelvic fins. Available meristic data and approximate measurements of this specimen are provided in Tables 1–8 (all measurements for this specimen are approximate because of distortion; those that could not be approximated are recorded as "?").

This specimen was not figured by Lesueur (1818) but was considered to be the type specimen, and a line drawing of it was provided by Fowler (1911, pl. 38, fig. 1; reproduced here as Fig. 3B), who noted (p. 604), "I figure this interesting example on account of its historical interest and rarity, as I have found no authentic American figures except Ryder's [1890] photographs." Fowler (1945) later doubted the identification of this specimen as Lesueur's holotype, citing absence of an original label and lack of any accession record of shortnose sturgeon from Lesueur at the ANSP. An unpublished drawing of *A. brevirostrum* made by Lesueur (labeled by Lesueur as *A. measus*) is curated at the Muséum du Havre, Le Havre, France (Roux, 1983), and is reproduced here on the cover.

TYPE LOCALITY AND DISTRIBUTION—The type locality for *A. brevirostrum* is the Delaware River (Lesueur, 1818), although the precise locality is unknown. Historically, *A. brevirostrum* inhabited coastal rivers along much of eastern North America (Fig. 4), from the Saint John River in New Brunswick, Canada, south to the St. Johns River in Florida (Vladykov & Greely, 1963; Dadswell et al., 1984; Wirgin et al., 2005). Kynard (1997) observed that its present range is divided into a northern and southern population, separated by a 400-km distance (between the Delaware River, New Jersey, to Cape Fear River, North Carolina). Because of the distance of the separation as well as differences in the preferred habitat of *A. brevirostrum* (riverine and coastal estuaries; see the section Natural History), Kynard (1997) hypothesized that there may be no interchange of adults (i.e., no genetic exchange) between the northern and southern populations. Some specimens of *A. brevirostrum* have been captured in the northern portion of the Chesapeake Bay, although genetic analyses strongly suggest that these have dispersed from the Delaware River population, perhaps through the Delaware-Chesapeake Canal (Wirgin et al., 2005). Based on telemetry studies, two adult females were found to use the Potomac River as both foraging grounds and for spawning, suggesting that this population may be rebuilding (Kynard et al., 2009).

EMENDED DIAGNOSIS—No simple combination of meristic or morphometric data is known to differentially diagnose and differentiate *A. brevirostrum* from other members of the genus *Acipenser*. However, the following characteristics in combination allow *A. brevirostrum* to be recognized as distinet from other sturgeons: small adult body size (i.e., *typically* less than 100 cm TL), relatively short snout (although with substantial variation in size and shape, ranging from pointed, particularly in juveniles, to blunt), anterior fontanelle in skull roof closed, dark blotches in juveniles (i.e., <30 cm TL), dorsal scutes 7–13, lateral scutes 21–35, ventral scutes 6–11, gill rakers 22–32, dorsal rays 38–42, and anal rays 18–24. This is one of two species of *Acipenser* from the east coast of North America, the other being *A. oxyrinchus*. Apart from size, specimens of *A. brevirostrum* can be easily distinguished from *A. oxyrinchus* by their relatively wider mouth and the dark color of the peritoneum (e.g., see diagnoses and descriptions provided by Vladykov & Greeley, 1963; Dadswell et al., 1984; Snyder, 1988; Musick et al., 1994; Hartel et al., 2002).

ETYMOLOGY—*brevis*, Latin, short; *rostrum*, Latin, snout.

NATURAL HISTORY—Much is known of the natural history of *A. brevirostrum*, in particular that of the Connecticut River population, through long-term studies by Boyd Kynard, Micah Kieffer, and their colleagues. We also have information on the relatively large population from the Hudson River (e.g., Bain, 1997). Much of this work and other data were summarized by Dadswell et al. (1984), Kynard (1997), Bemis and Kynard (1997), and the Shortnose Sturgeon Recovery Team for the National Marine Fisheries Service (NMFS, 1998), so we present here only a brief overview of the natural history of *A. brevirostrum*.

Acipenser brevirostrum is a relatively small species of sturgeon (longest on record is 1220 mm FL, 1430 mm TL; Dadswell et al., 1984). In general, this species is almost entirely riverine or estuarine in habitat, although pronounced latitudinal variation exists in the degree of anadromy (Kynard, 1997). Northern populations (i.e., Saint John, Kennebec, Androscogin, and Merrimack rivers) remain in estuarine environments almost the entire year and may overwinter in 30% seawater. In the middle part of their range (i.e., from the Connecticut River to the Delaware River), individuals of *A. brevirostrum* rarely leave freshwater. Southern populations (i.e., south of Cape Fear, North Carolina) spend the most time in salt water, rarely leaving the estuary to enter the rivers to forage or breed. Kynard (1997, p. 324) hypothesized that this variation in anadromy reflected "bioenergetic adaptations for obtaining the optimal environment for foraging and growth," noting that "an acceptable thermal regime in fresh water is shortest in northern rivers, longest in north-central rivers where fish spend the most time in fresh water, and may be intermediate in southern rivers."

Based on the genetic differences among populations, Walsh et al. (2001) estimated that about seven females per generation migrated between the Kennebec and Androsoggin river populations, which share a common estuary, and about only one female per generation migrated between either of these rivers and the much more remote Hudson River population. If this trend of lower genetic exchange between populations that are further apart is extrapolated to the entire range, this might provide a mechanism for the maintenance of morphological disparity between northern and southern populations (E.J.H., pers. obs.; see also Hilton & Bemis, in press).

REMARKS—In his description, Lesueur (1818) described three "varieties" of *A. brevirostrum* that differed from one another in characters such as meristic data, position and shape of scutes, and the shape of the snout; these likely represent individual or ontogenetic variations. Lesueur (1818, p. 392) noted, "This species, which is not

FIG. 5. *Acipenser brevirostrum*, whole alcohol-preserved juvenile specimen (VIMS 11614; 225 mm SL), approximately three-year-old captive-reared specimen spawned from Connecticut River adults at the Conte Anadromous Fish Research Lab (Turners Falls, Massachusetts). Note the spotting pattern on the dorsal and lateral surfaces. (**A**) Dorsal, (**B**) lateral, and (**C**) ventral views. Anterior to left.

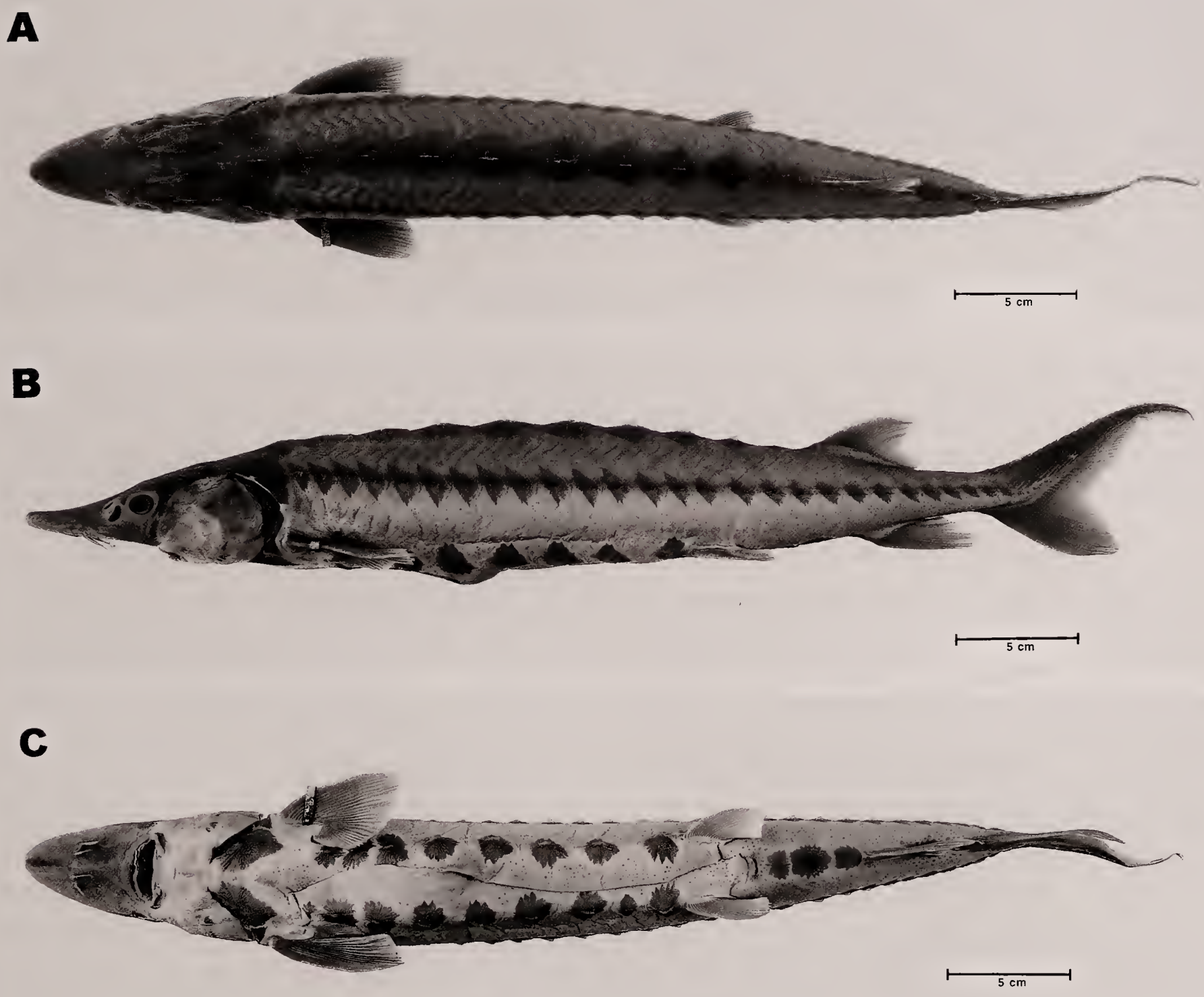


FIG. 6. *Acipenser brevirostrum*, whole alcohol-preserved specimen (MCZ 54265; 405 mm SL), from the Connecticut River of western Massachusetts. (**A**) Dorsal, (**B**) lateral, and (**C**) ventral views. Anterior to left.

TABLE 1. Sex and body measurements for a growth series of *Acipenser brevirostrum*.

Specimen no. (SL)	Sex	Total length	Fork length (as %SL)	Prepectoral fin length (as %SL)	Prepelvic fin length (as %SL)	Predorsal fin length (as %SL)	Preanal fin length (as %SL)
VIMS 12101 (no SL)	?	42.9 mm	no fork length	14.1 mm (—)	24.4 mm (—)	26.9 mm (—)	27.8 mm (—)
VIMS 12082 (no SL)	?	58.5 mm	no fork length	18.3 mm (—)	32.9 mm (—)	37.0 mm (—)	38.2 mm (—)
FMNH 112215 (50.9 mm)	?	60.5 mm	no fork length	20.4 mm (40%)	35.5 mm (70%)	39.1 mm (77%)	43.6 mm (86%)
VIMS 12086 (71.1 mm)	?	89.2 mm	no fork length	28.0 mm (39%)	50.5 mm (71%)	56.9 mm (80%)	58.8 mm (83%)
FMNH 112918 (80.0 mm)	?	95.8 mm	no fork length	29.8 mm (37%)	56.5 mm (70%)	62.5 mm (78%)	64.8 mm (81%)
FMNH 112916 (85.5 mm)	?	108 mm	no fork length	30.7 mm (36%)	58.9 mm (69%)	66.9 mm (78%)	70.1 mm (82%)
FMNH 112917 (104 mm)	?	130 mm	115 (110%)	37.4 mm (36%)	72.6 mm (70%)	81.7 mm (78%)	86.7 mm (83%)
VIMS 12087 (251 mm)	?	325 mm	274 mm (109%)	79.7 mm (32%)	174 mm (69%)	197 mm (78%)	205 mm (82%)
MCZ 54167 (472 mm)	?	545 mm	500 mm (106%)	120 mm (25%)	315 mm (67%)	380 mm (81%)	400 mm (85%)
FMNH 117461 (640 mm)	male	785 mm	670 mm (105%)	157 mm (25%)	415 mm (65%)	500 mm (78%)	525 mm (82%)
ANSP 16953 holotype (690 mm)	?	800 mm (est.)	725 mm (105%)	125 mm (est.) (18% est.)	? (?)	565 mm (82%)	588 mm (85%)
FMNH 112212 (710 mm)	?	870 mm	750 mm (106%)	150 mm (21%)	450 mm (63%)	525 mm (74%)	580 mm (82%)
FMNH 112913 (755 mm)	?	885 mm	795 mm (105%)	180 mm (24%)	505 mm (67%)	600 mm (79%)	635 mm (84%)
UMA F10578 (899 mm)	male	1059 mm	948 mm (105%)	213 mm (24%)	595 mm (66%)	708 mm (79%)	752 mm (84%)
FMNH 113538 (960 mm)	female	1120 mm	1025 mm (107%)	175 mm (18%)	650 mm (68%)	765 mm (80%)	815 mm (85%)

TABLE 2. Head measurements and meristic data for a growth series of *Acipenser brevirostrum*.

Specimen no. (SL)	Head length (as %SL)	Prenares length (as % SL)	Preorbital length (as %SL)	Skull width (as %SL)	Skull length (as %SL)	Exposed portion of left parietal (as %SL)	Exposed portion of right parietal (as %SL)
VIMS 12101 (no SL)	13.3 mm (—)	5.3 mm (—)	7.4 mm (—)	4.2 mm (—)	14.6 mm (—)	2.1 mm (—)	1.7 mm (—)
VIMS 12082 (no SL)	16.7 mm (—)	7.8 mm (—)	10.3 mm (—)	5.5 mm (—)	19.9 mm (—)	3.0 mm (—)	3.5 mm (—)
FMNH 112215 (50.9 mm)	19.2 mm (38%)	7.9 mm (16%)	9.7 mm (19%)	6.0 mm (12%)	20.7 mm (41%)	5.4 mm (11%)	6.4 mm (13%)
VIMS 12086 (71.1 mm)	27.5 mm (39%)	13.9 mm (20%)	15.4 mm (22%)	7.8 mm (11%)	30.5 mm (43%)	7.4 mm (10%)	8.6 mm (12%)
FMNH 112918 (80.0 mm)	26.4 mm (33%)	12.1 mm (15%)	16.4 mm (21%)	7.0 mm (9%)	31.9 mm (40%)	8.2 mm (10%)	6.9 mm (9%)
FMNH 112916 (85.5 mm)	28.4 mm (33%)	13.4 mm (16%)	16.5 mm (19%)	9.2 mm (11%)	32.1 mm (38%)	8.9 mm (10%)	9.2 mm (11%)
FMNH 112917 (104.3 mm)	34.1 mm (33%)	16.1 mm (15%)	20.7 mm (20%)	9.8 mm (9%)	38.0 mm (36%)	9.4 mm (9%)	7.6 mm (7%)
VIMS 12087 (251 mm)	74.9 mm (30%)	26.1 mm (10%)	34.5 mm (14%)	27.5 mm (11%)	85.6 mm (34%)	26.5 mm (11%)	21.6 mm (9%)
MCZ 54167 (472 mm)	115 mm (24%)	39.0 mm (8%)	50.0 mm (11%)	45.0 mm (10%)	129 mm (27%)	42 mm (9%)	37 mm (8%)
FMNH 117461 (640 mm)	145 mm (23%)	45% (7%)	65 mm (10%)	62 mm (10%)	176 mm (28%)	60 mm (9%)	59 mm (9%)
ANSP 16953 holotype (690 mm)	120 mm (17%)	15 mm (2%)	? (?)	50 mm (7%)	? (?)	? (?)	? (?)
FMNH 112212 (710 mm)	137 mm (19%)	39 mm (5%)	32 mm (5%)	60 mm (8%)	167 mm (24%)	49 mm (7%)	46 mm (6%)
FMNH 112913 (755 mm)	165 mm (22%)	39 mm (5%)	60 mm (8%)	65 mm (9%)	187 mm (25%)	61 mm (8%)	57 mm (8%)
UMA F10578 (899 mm)	195 mm (22%)	55 mm (6%)	80 mm (9%)	75 mm (8%)	190 mm (21%)	65 mm (7%)	68 mm (8%)
FMNH 113538 (960 mm)	165 mm (17%)	22 mm (2%)	45 mm (5%)	83 mm (9%)	215 mm (22%)	77 mm (8%)	73 mm (8%)

the object of a special fishery, is nevertheless more sought after, and commands a higher price, than the large common species [= *A. oxyrinchus*], which attains to the length of about ten feet. The *A. brevirostrum*, and its varieties, are brought to the Philadelphia market in the vernal season, and fetch from twenty-five to seventy-five cents a-piece. They are eaten by the common people only"; Ryder (1890, p. 238), however, commented that *A. brevirostrum* "does not seem to be eaten at all by the present generation of Delaware fishermen."

While the shortnose sturgeon is the most commonly used vernacular name for *A. brevirostrum* (Nelson et al., 2004), other names include the shortnosed sturgeon, pinkster, roundnoser, bottlenose, mammose, salmon sturgeon, soft-shell sturgeon, and, inappropriately, lake sturgeon (Dadswell et al., 1984).

An annotated bibliography of literature related to *A. brevirostrum* was published by Hoff (1979). Dadswell et al. (1984) published a synopsis of the biology of *A. brevirostrum*, and a short review of the species was published by Vecsei and Peterson (2000).

Materials Examined—Materials examined include alcohol-stored specimens (a), sputter-coated specimens (SEM), dry skeletons (ds), and cleared and stained specimens (cs). Most specimens examined were collected in the Connecticut River of western Massachusetts, and all cleared and stained specimens less than 470 mm SL were raised from artificially spawned adults from this population. A nearly complete posthatching developmental series of *A. brevirostrum* was examined during this study. These specimens were derived primarily from two sets. One set of specimens came from spawnings conducted at the USGS/Leetown Science Center S. O. Conte Anadromous Fish Laboratory (CAFL), Turners Falls, Massachusetts, by Drs. Alan M. Richmond and Boyd Kynard during the early and middle 1980s (see Richmond & Kynard, 1995). These specimens were supplemented by a new series spawned and raised by Erika Henyey-Parker and Boyd Kynard, also at the CAFL, in the spring of 2003. These latter specimens were fixed by immersion in neutrally buffered 4% paraformaldehyde. Specific specimens (i.e., those that are illustrated or are included in our tables) from these series are provided with individual museum numbers; the remaining specimens of each series (both prepared and unprepared specimens) are cataloged as a single lot: 1980s specimens are uncataloged at UMA, and the 2003 series is cataloged as VIMS 12090 (n = 73 alcohol specimens) and VIMS 12091 (n = 45 cleared and stained specimens). These early stages were supplemented by larger, captive-raised specimens (e.g., 10–35 cm SL) from several years of spawning (reared by Henyey-Parker and Kynard in the late 1990s and early 2000s).

The following specimens of *A. brevirostrum* were examined (standard lengths [SL] are provided; if no SL exists because of ontogenetic stage, total length [TL] is given):

ANSP 16953 (holotype; 1 stuffed specimen; 690 mm SL); ANSP 148036 (1 a, 540 mm SL); ANSP 148041 (1 a, 595 mm SL); ANSP 148039 (1 a, 700 mm SL); FMNH 112209 (1 ds, 740 mm SL); FMNH 112210 (1 ds, 805 mm SL); FMNH 112211 (1 ds, 537 mm SL); FMNH 112212 (1 ds, 710 mm SL); FMNH 112213 (1 ds, 630 mm SL); FMNH 112214 (1 ds, 763 mm SL); FMNH 112215 (1 cs, 50.9 mm SL); FMNH 112913 (1 ds, 755 mm SL); FMNH 112914 (1 ds, 655 mm SL); FMNH 112915 (1 cs, 605 mm SL); FMNH 112916 (1 cs, 85.5 mm SL); FMNH 112917 (1 cs, 85.5 mm SL); FMNH 112918 (1 cs, 80 mm SL); FMNH 113538 (1 ds, 960 mm SL); FMNH 117461 (1 ds, 640 mm SL); MCZ 54167 (1 cs, 472 mm SL); MCZ 54265 (1 a, 405 mm SL); UMA F10016 (1 ds, 600 mm SL); UMA F10018 (1 ds, 725 mm SL); UMA F10020 (1 ds, 880 mm SL); UMA F10023 (1 ds, 605 mm SL); UMA F10024 (1 ds, 885 mm SL); UMA F10431 (1 ds, 930 mm SL); UMA F10461 (1 ds, 825 mm SL); UMA F10521 (1 ds, 640 mm SL); UMA F10547 (1 ds, 915 mm SL); UMA F10578 (1 ds, 899 mm SL); UMA F10579 (1 ds, 880 mm SL); USNM 125816 (1 a, 423 mm SL); USNM 125817 (1 a, 525 mm SL); USNM 125818 (1 a, 480 mm SL); VIMS 11614 (1 a, 225 mm SL); VIMS 12071 (1 ds, 705 mm SL); VIMS 12072 (1 ds, 940 mm SL); VIMS 12073 (1 ds, 660 mm SL); VIMS 12074 (1 ds, 695 mm SL); VIMS 12075 (1 cs, 19.8 mm TL); VIMS 12076 (1 cs, 22.1 mm TL); VIMS 12077 (1 cs, 21.9 mm TL); VIMS 12078 (1 cs, 23.3 mm TL); VIMS 12079 (1 cs, 23.8 mm SL); VIMS 12080 (1 cs, 57.4 mm TL); VIMS 12081 (1 cs, 58.7 mm TL); VIMS 12082 (1 cs, 58.5 mm TL); VIMS 12084 (1 cs, 127 mm SL); VIMS 12085 (1 SEM; est. 18.5 mm TL); VIMS 12086 (1 cs, 71 mm SL); VIMS 12087 (1 cs, 251 mm SL); VIMS 12088 (1 cs, 30.5 mm TL); VIMS 12089 (1 cs, 41.6 mm TL); VIMS 12090 (73 a, 9.5–50.8 mm TL); VIMS 12091 (45 cs, 14.8–59.6 mm TL); VIMS 12092 (7 cs, est. 35.0–46.1 mm TL); VIMS 12093 (7 cs, 40.2–70.7 mm TL); VIMS 12094 (54 a, est. 23.0–62.0 mm TL); VIMS 12095 (9 a, 37.3–59.4 mm TL); VIMS 12096 (3 a, 25.8–28.6 mm TL); VIMS 12101 (1 cs, 42.9 mm TL); VIMS 12102 (1 cs, 166 mm SL). Also, specimens are listed in Hilton (2002a, 2005) and Hilton and Bemis (1999, in press).

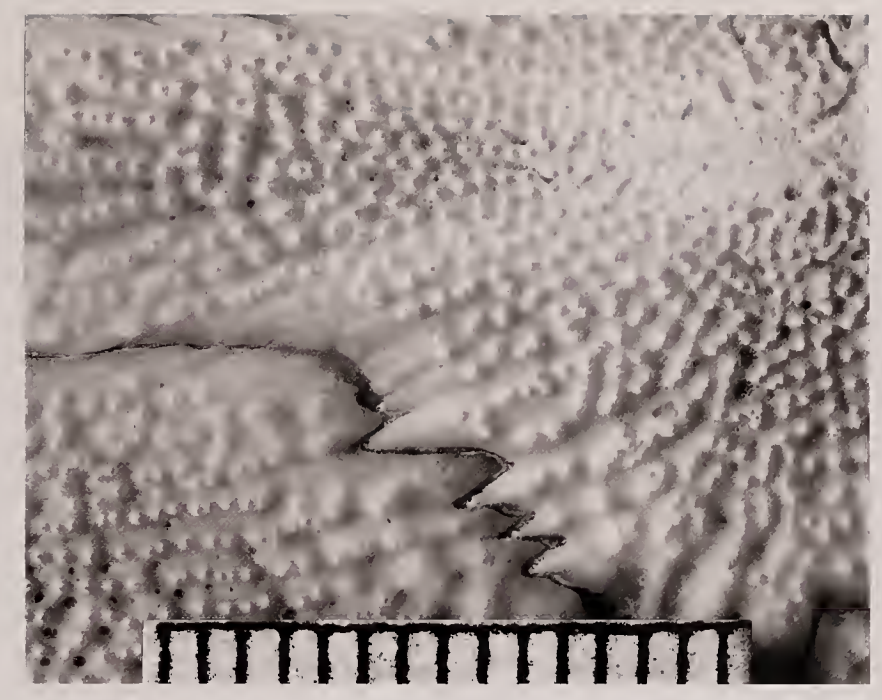


Fig. 7. *Acipenser brevirostrum*, close-up of ornament on dermal skull bones, from UMA F10431 (male, 930 mm SL). Anterior to left. Scale in millimeters.

Anatomical Descriptions

The ultimate aim of the zoologist and botanist, however, is, or should be, not the description of so many new species in a lifetime, but the grouping of animals and plants according to their natural affinities, and for this purpose a wider knowledge of morphology is necessary.

—Walter George Ridewood (1895, p. 260)

It may sound strange in the ears of some that the elements that go to make up the mouth of such a creature as the Sturgeon should be boldly named by the very terms used in the description of the human palate, mouth, and throat; but it must be remembered that a knowledge of the true representative elements, in forms so wide apart, has not come of itself to anatomists. There has been long and anxious work, by many skilled workers, to bring this about.

—William Kitchen Parker (1873, p. 257)

Counts and Measurements

Counts and measurements for a growth series of *A. brevirostrum* are provided in Tables 1–8. There is meristic and morphometric variation among different populations of *A. brevirostrum* (Dadswell et al., 1984; E.J.H., pers. obs.). Significant differences in morphometric and meristic data, including head and snout length and mouth width, among specimens from three northern populations (the Kennebec, Androscoggin, and Hudson rivers) were found by Walsh et al. (2001). For this reason (i.e., to avoid confounding effects of geographic or clinal variation), the growth series for which we tabulate meristic and morphometric data consists of specimens from a single population (the Connecticut River or captively reared progeny from Connecticut River adults), with the exception of the holotype. A more detailed analysis of morphometric and meristic variation (of these and other variables) for the Connecticut River population of *A. brevirostrum* is presented elsewhere (Hilton & Bemis, in press). The data presented in Tables 1–8 also will form the basis of

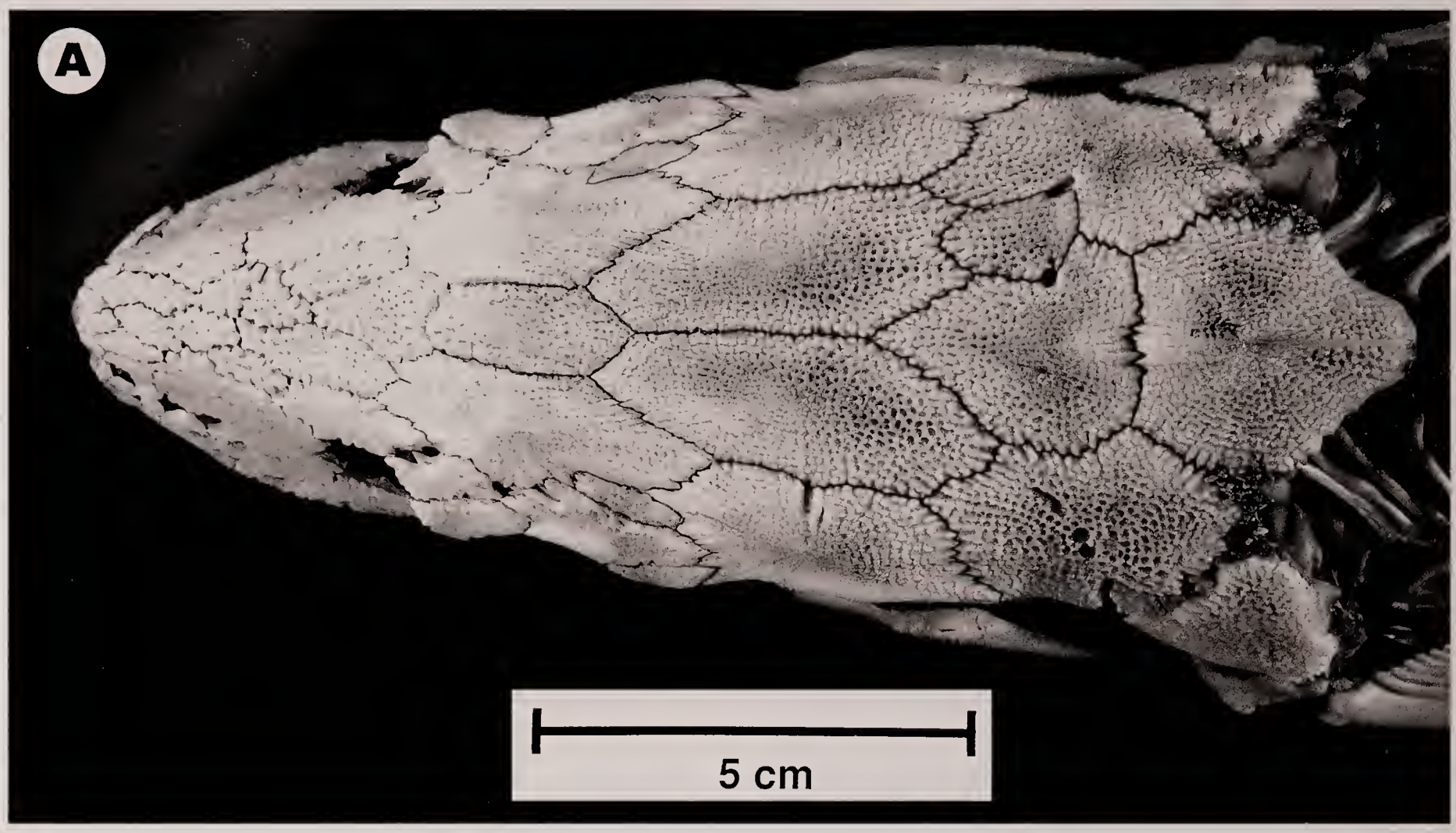
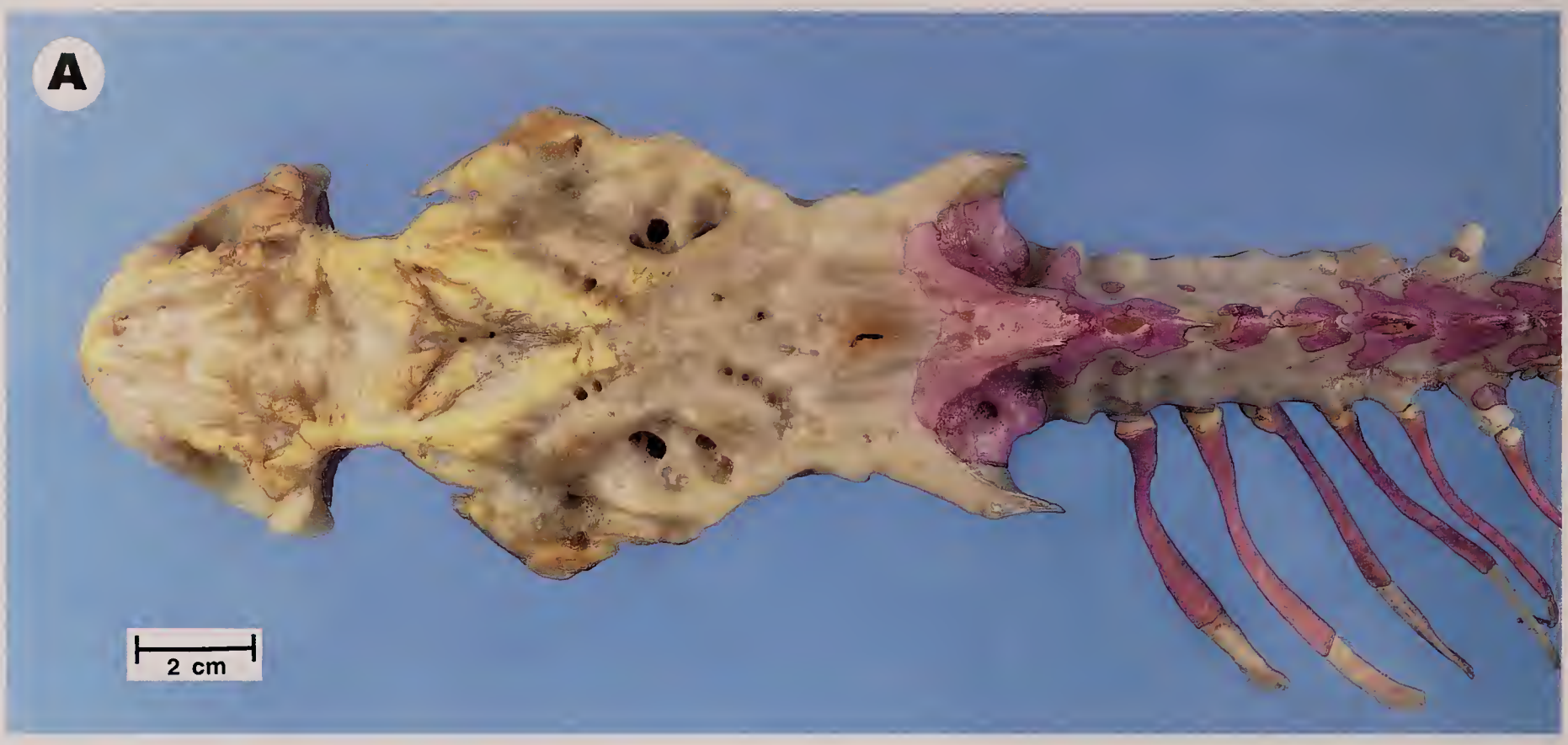


FIG. 8. *Acipenser brevirostrum*, skull and pectoral girdle of adult in dorsal view, from FMNH 112212 (sex unknown, 710 mm SL). (**A**) Photograph and (**B**) line drawing. Slight distortion of specimen due to displacement of elements during drying. Anterior to left. Abbreviations found on pages 8–9.

FIG. 9. *Acipenser brevirostrum*, dermal bones of the skull roof in dorsal view, from UMA F10431 (male, 930 mm SL). (**A**) Photograph and (**B**) line drawing. Anterior to left. Abbreviations found on pages 8–9.



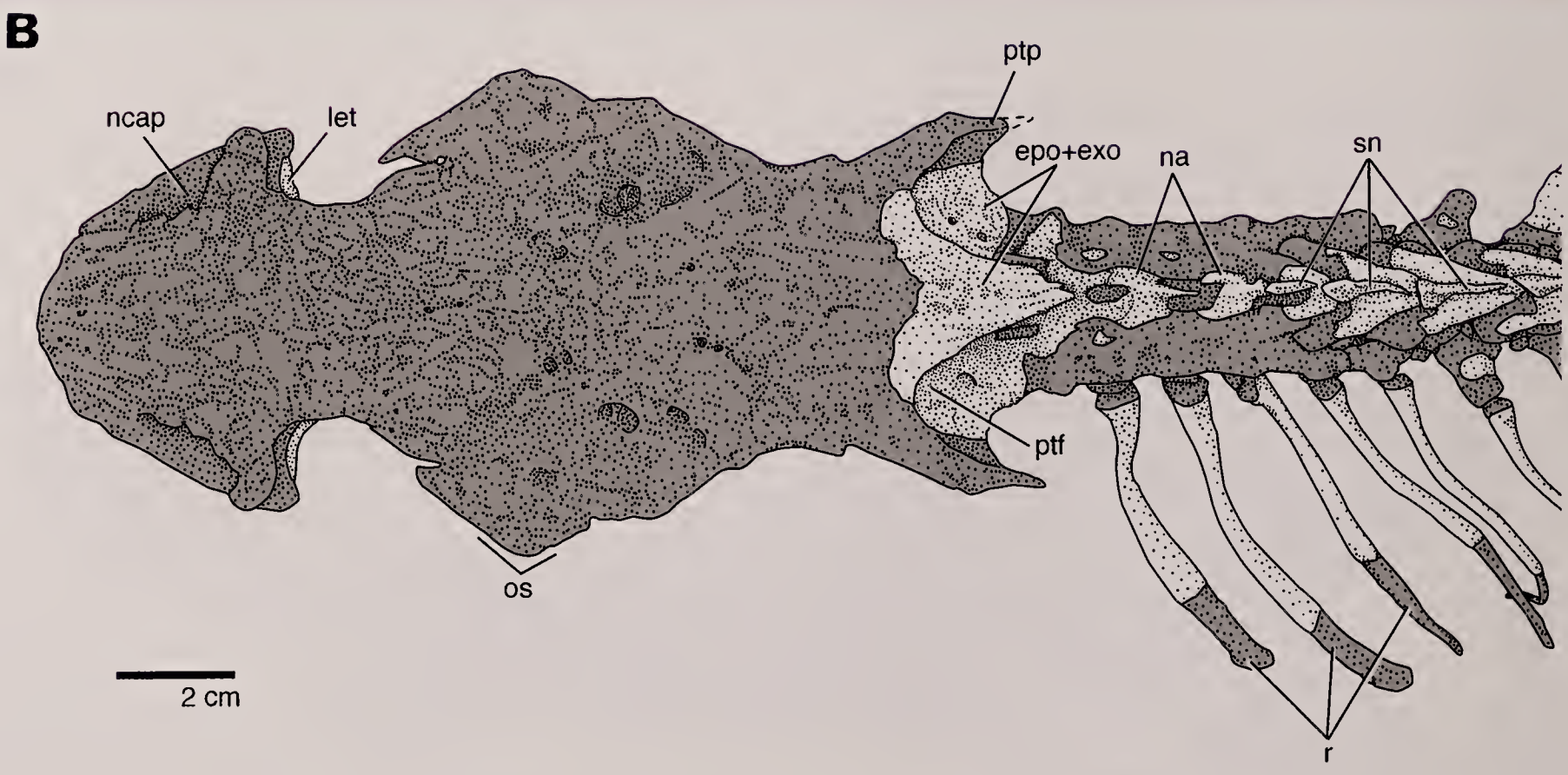


FIG. 10. *Acipenser brevirostrum*, neurocranium in dorsal view, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing. In photo, bone is stained red, and cartilage appears white; in drawing bone is white, and cartilage is gray. Anterior to left. Abbreviations found on pages 8–9.

ongoing and future comparative studies that are aimed at better differentially diagnosing all species of Acipenseridae.

Bones of the Skull Roof and Circumorbital Region

The dermal bones of the skull are illustrated in Figures 7–51. All dermal bones of the skull roof are ornamented with a dense array of pits and ridges that are formed by the fusion of denticle or tubercle-like elements to the underlying bone. The pattern of skull roofing bones in acipenserids is marked by extreme variation (see Figs. 24, 25; see also Jarvik, 1948, fig. 18; Jollie, 1980, fig. 8; Hilton & Bemis, 1999, fig. 5). Of the bones that form the "stable" elements of the functional dermal skull roof (i.e., those elements, including axial and appendicular elements incorporated into the skull, that are readily comparable among specimens), seven are paired (frontals, parietals, dermopterotics, posttemporals, supratemporals, supraorbitals, and nasals), and two are median (median extrascapular and first dorsal scute). A series of lateral extrascapulars is present in most specimens, although substantial variation in the number, shape, and arrangement of these elements, including bilateral asymmetry, exists. The stable circumorbital bones include the dermosphenotic, the postorbital, and the jugal. The anamestic bones (i.e., those bones that are independent of the cephalic sensory canal system) of the snout will be discussed in the section Anamestic Bones of the Dorsal Rostrum, and the dermal elements of the anterior infraorbital sensory canal (i.e., the rostral sensory canal) will be discussed in the section Braincase.

The posteriormost element of the skull roof is the first (i.e., the anteriormost) dorsal scute (**ds1**, Figs. 8, 9, 11–18), which, although not part of the skull proper, is so fully incorporated into the adult skull that it is discussed in this section and illustrated with elements of the skull roof. This single median bone lies in the midline of the skull and is roughly pentagonal in shape, although its exact form is variable (cf. Figs. 8, 9). The first dorsal scute contacts the left and right posttemporals anterolaterally and the median extrascapular anteriorly, by which it is slightly overlapped dorsally, leaving a small area of unornamented bone along its anterior margin. The first dorsal scute begins its development in series with the free dorsal scutes (also in *Scaphirhynchus*; Findeis, 1993; see the section Scutes) and is autogenous in early development but is contacted anterolaterally by the posttemporals by about 37 mm TL.

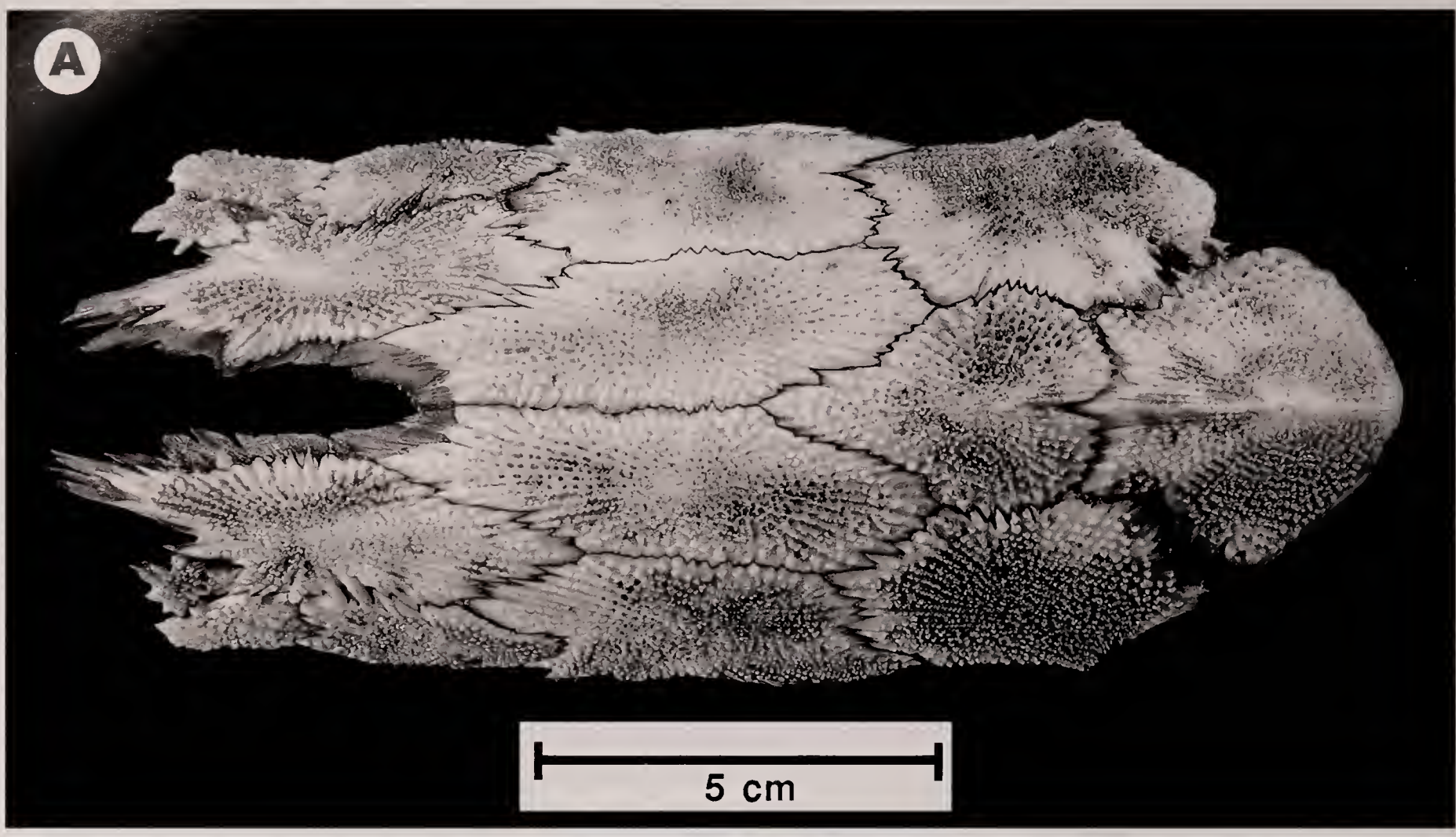
Like the first dorsal scute, the posttemporal bones (**pt**, Figs. 8, 9, 11–18), which are the dorsalmost elements of the pectoral girdle, become incorporated into the skull and form the posterolateral margins of the functional skull roof. The posttemporal is ossified in specimens greater than or equal to 20.5 mm TL. Each posttemporal contacts the extrascapular bones (median and, if present, lateral extrascapulars; **excm** and **excl**, respectively) medially, the parietal anteromedially, and the dermopterotic anteriorly. There is a slight overlap of the posttemporal by the first dorsal scute, reflected in the unornamented posterior margin of the posttemporal (Fig. 12). The most prominent feature of the ventral surface of the posttemporal is a large ventral lamella of bone (**pt(v)**, Figs. 13, 14), which grows ventrally to cover the lateral surface of the occipital region of the chondrocranium. This ventral lamella is obliquely oriented, following the ventral surface of the posttemporal processes of the chondrocranium.

Anterior to the first dorsal scute lie the extrascapular bones, the posteriormost of the true skull roofing bones. The unpaired median extrascapular (**excm**, Figs. 8, 9, 11–18) is present in all individuals and contacts the first dorsal scute posteriorly, the parietals anteriorly, and the posttemporals and, if present, the lateral extrascapular(s) laterally (in one specimen of *A. fulvescens* studied here, FMNH 98256, the median extrascapular is divided into a paired element; the left is slightly smaller than the right). The median extrascapular bone, which was first observed in a 42.3 mm TL specimen, carries the occipital sensory canal, which loops forward in the midline where the left and right portions of the canal meet. In ventral view, the median extrascapular is almost entirely covered by the posterior extensions of the parietal bones (Fig. 13). Although there is much individual variation in its overall shape (cf. Figs. 8, 9), this bone is widest posteriorly, tapers to a point anteriorly, and is nearly triangular in shape in most specimens. In one specimen (UMA F10579), the median extrascapular is divided into an anterior triangular bone and posterior rectangular bone. The anterior portion of the median extrascapular extends forward, separating the posterior one-third to one-half of the exposed portions of the left and right parietals. In one specimen (FMNH 112211; Figs. 24F, 25F), however, it extends to separate the anterior portion of the parietals.

Variably present in *A. brevirostrum* and in acipenserids generally are a series of irregularly shaped and numbered lateral extrascapulars (**excl**, Figs. 8, 9). These bones, which may or may not form around the occipital sensory canal, lie intercalated between the median extrascapular and the posttemporal and are variable in number, with up to three present on each side and substantial bilateral asymmetry in number, shape, and position. In most specimens, there are anamestic bones present in this region that may also be referred to as lateral extrascapulars (e.g., Findeis, 1993; Hilton & Bemis, 1999).

The large dermopterotics (**dpt**, Figs. 8, 9, 11–18) form the anterior half of the postorbital margin of the skull roof and are the first bones of the skull roof to develop; we first found them ossified in a 21.0 mm TL specimen as thin splints of bone associated with the supratemporal sensory canal. The bone around the sensory canal broadens during ontogeny, and these elements grow to contact the posttemporals posteriorly and the postorbitals, dermosphenotics, and frontals anteriorly. There is an elongate suture between the dermopterotic and the parietal. On its ventral surface, the dermopterotic bears a short, ventrally directed lamina that crosses the middle portion of the bone obliquely (Figs. 13, 14). This irregularly shaped lamina grows from the ventral surface of the main portion of the dermopterotic adjacent to the lateral margin of the chondrocranium in the otic region.

The paired parietals of *A. brevirostrum* (**pa**, Figs. 8, 9, 11–18) are ossified in specimens 23.2 mm TL and longer and make up a major component of the posterior portion of the adult skull roof. The parietals develop early in ontogeny and first appear on the skull roof as a pair of small, denticle-like spots of bone that then grow anteriorly as a thin "string" of bone (this anterior growth was noted in a 27.6 mm TL specimen). In adults, the parietals contact the median extrascapular and the posttemporals posteriorly, the dermopterotics laterally, and the frontals and median anamestic bones of the snout anteriorly. The left and right parietals typically meet in the midline at an elongate suture; only a single specimen studied here (FMNH 112211; Figs. 24F, 25F) was observed to have the left and right parietals separated, predominantly by a greatly elongated median extrascapular. Each parietal bears



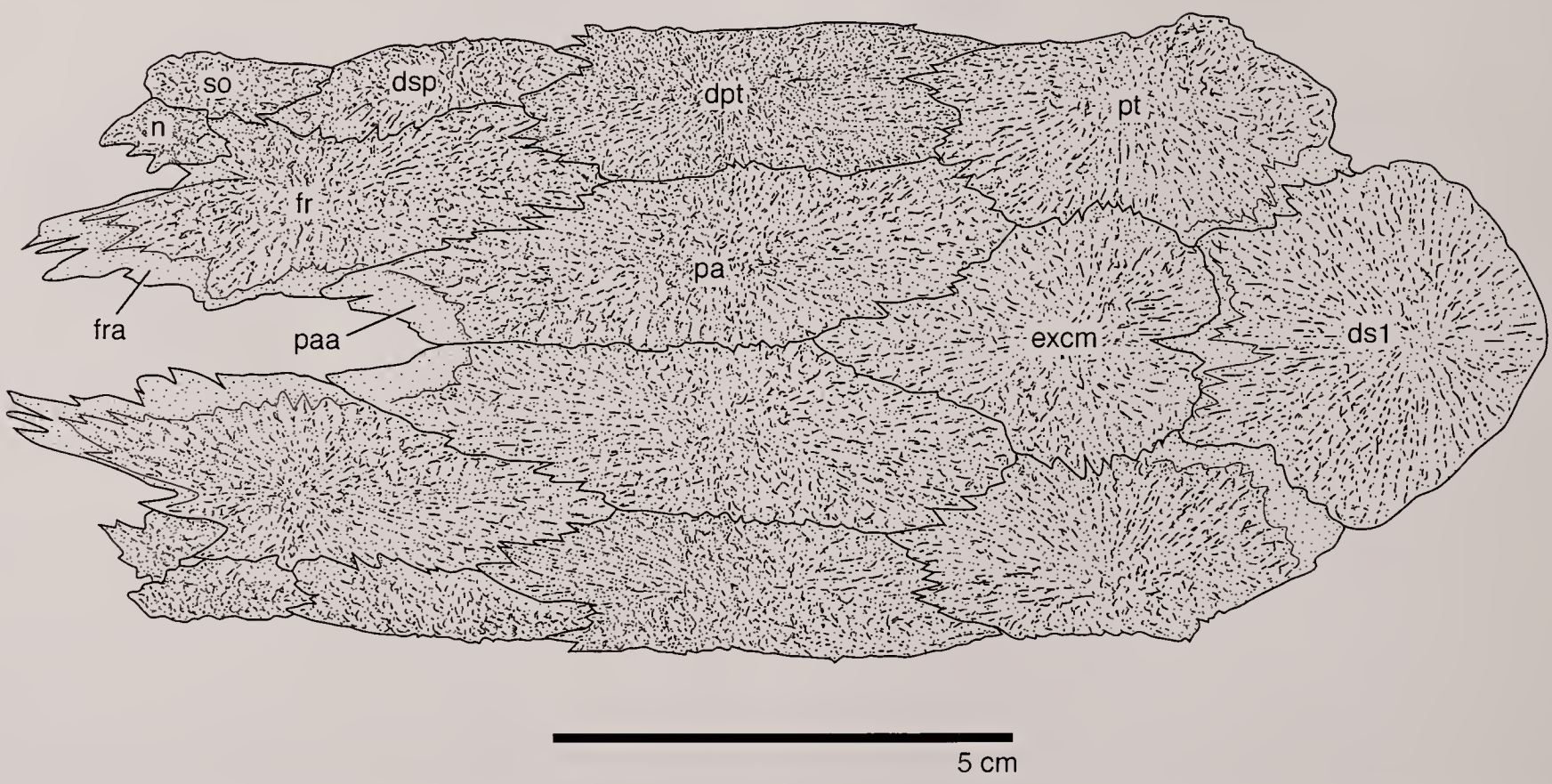


FIG. 11. *Acipenser brevirostrum*, "stable" dermal bones of the skull roof (i.e., those elements that can be identified in every individual) in dorsal view, from UMA F10547 (male, 915 mm SL). **(A)** Photograph and **(B)** line drawing. Note that the anterior series of anamestic rostral bones was removed from this specimen. Anterior to left. Abbreviations found on pages 8–9.

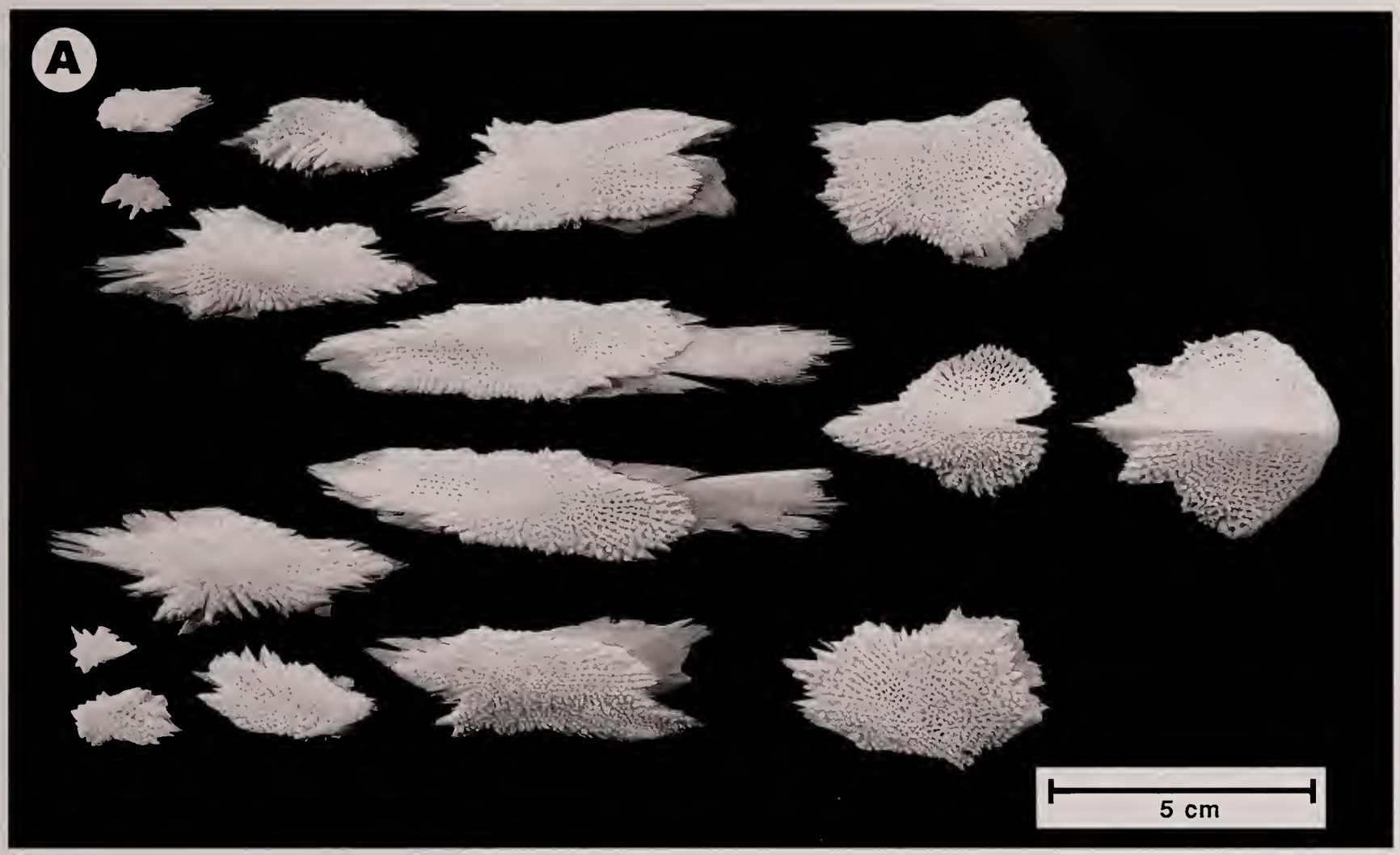
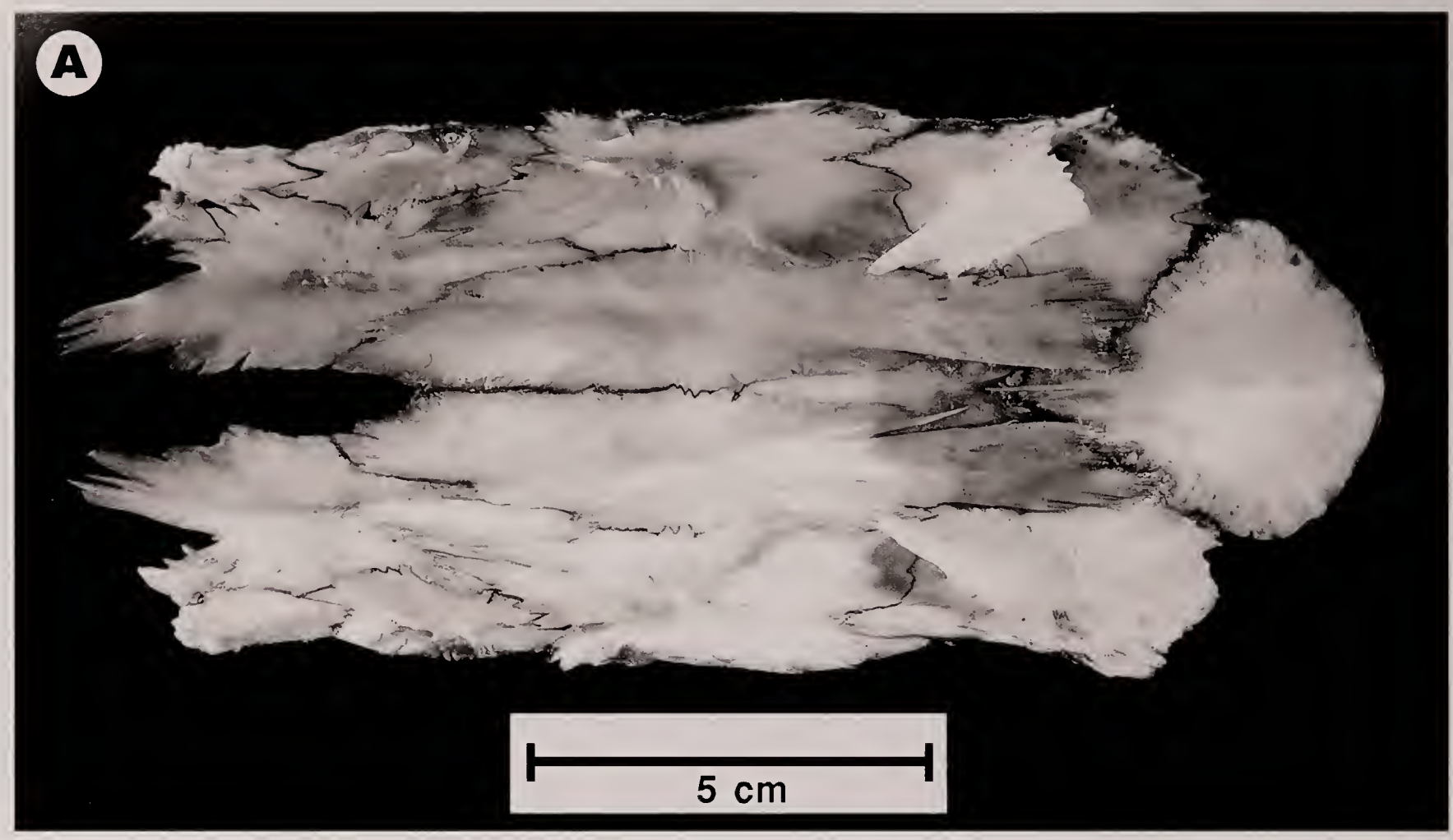


FIG. 12. *Acipenser brevirostrum*, disarticulated "stable" dermal bones of the skull roof (i.e., those elements that can be identified in every individual) in dorsal view, from UMA F10547 (male, 915 mm SL). (**A**) Photograph and (**B**) line drawing. Note that the anterior series of anamestic rostral bones was removed from this specimen. Anterior to left. Abbreviations found on pages 8–9.



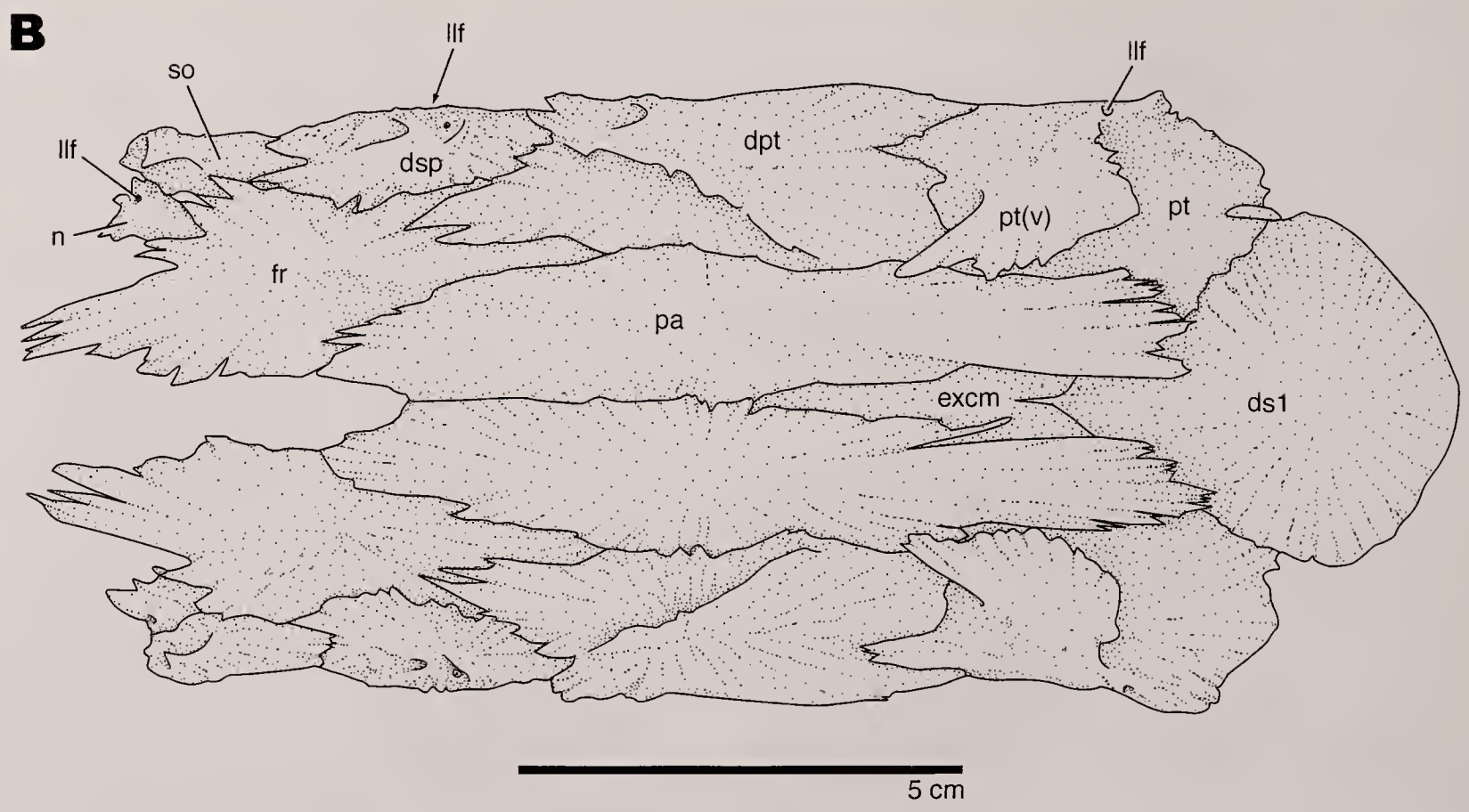


FIG. 13. *Acipenser brevirostrum*, "stable" dermal bones of the skull roof (i.e., those elements that can be identified in every individual) in ventral view, from UMA F10547 (male, 915 mm SL). (**A**) Photograph and (**B**) line drawing. Note that the anterior series of anamestic rostral bones was removed from this specimen. Anterior to left. Abbreviations found on pages 8–9.

FIG. 14. *Acipenser brevirostrum*, disarticulated "stable" dermal bones of the skull roof (i.e., those elements that can be identified in every individual) in ventral view, from UMA F10547 (male, 915 mm SL). (**A**) Photograph and (**B**) line drawing. Note that the anterior series of anamestic rostral bones was removed from this specimen. Anterior to left. Abbreviations found on pages 8–9.

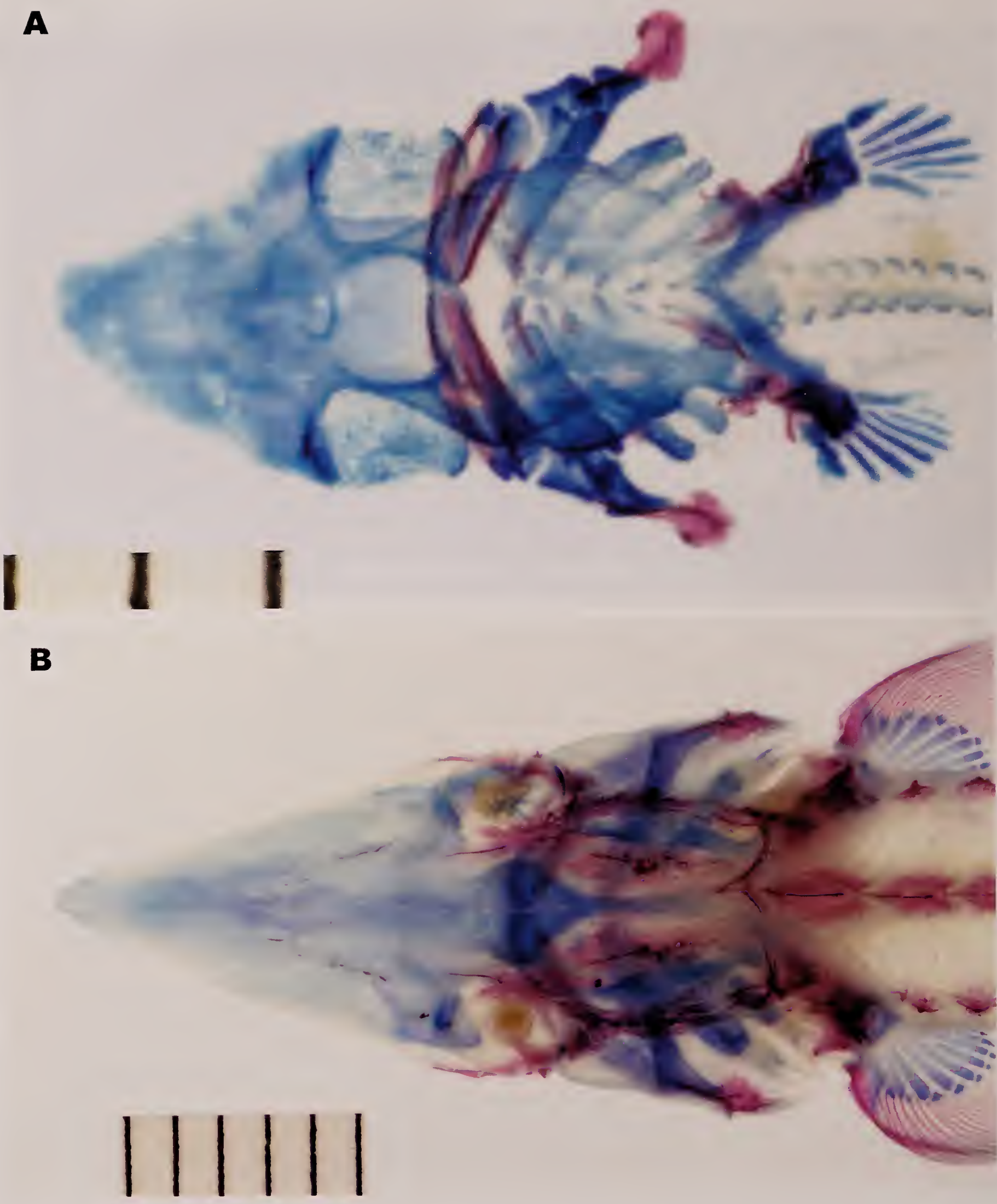


FIG. 15. *Acipenser brevirostrum*, skull and pectoral girdle at early stages of development in dorsal view. (**A**) VIMS 12077 (21.9 mm TL). (**B**) VIMS 12082 (58.5 mm TL). Scale in millimeters. Anterior to left. Abbreviations found on pages 8–9.

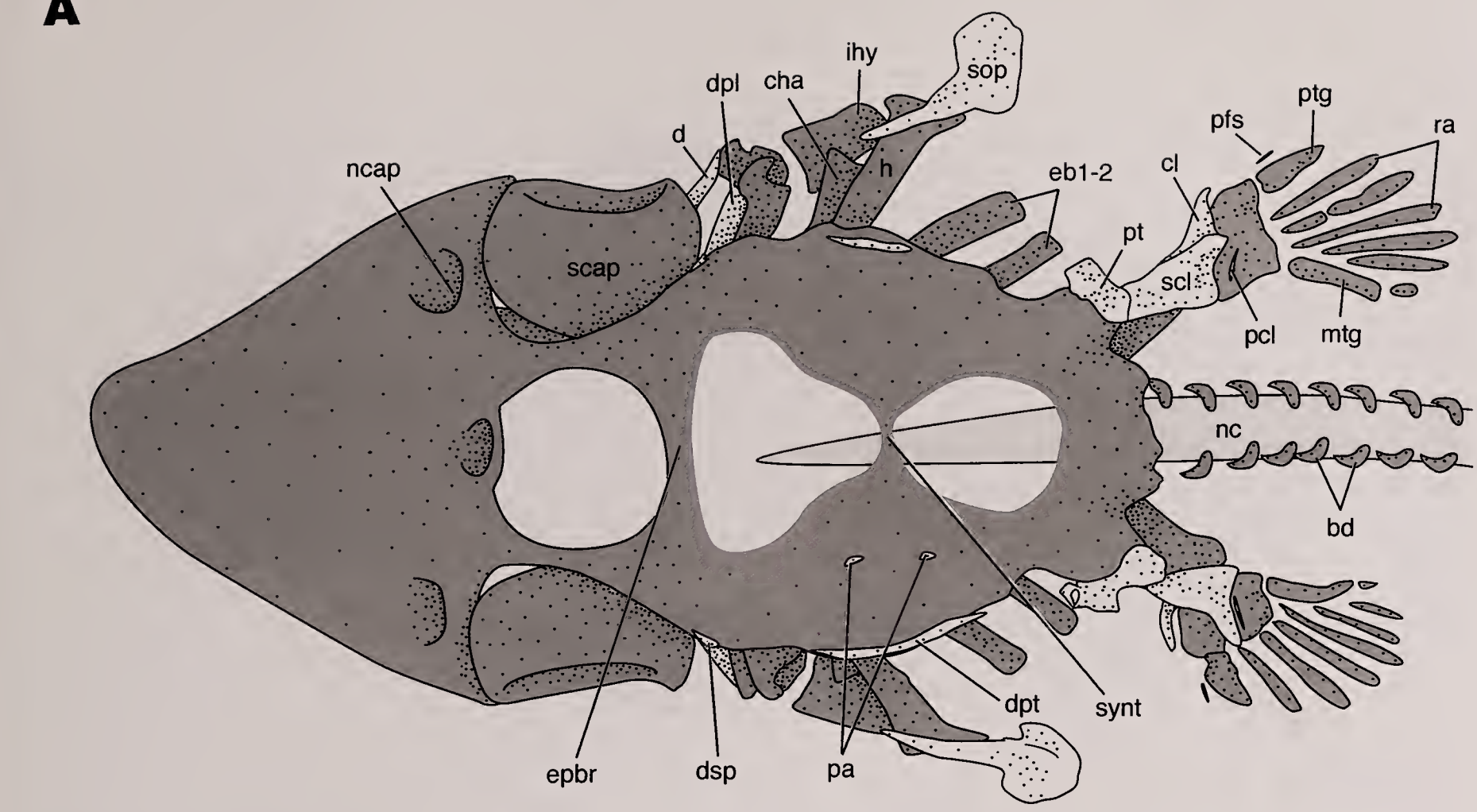


FIG. 16. *Acipenser brevirostrum*, skull and pectoral girdle at early stages of development in dorsal view. Line drawing of Figure 15. Abbreviations found on pages 8–9.

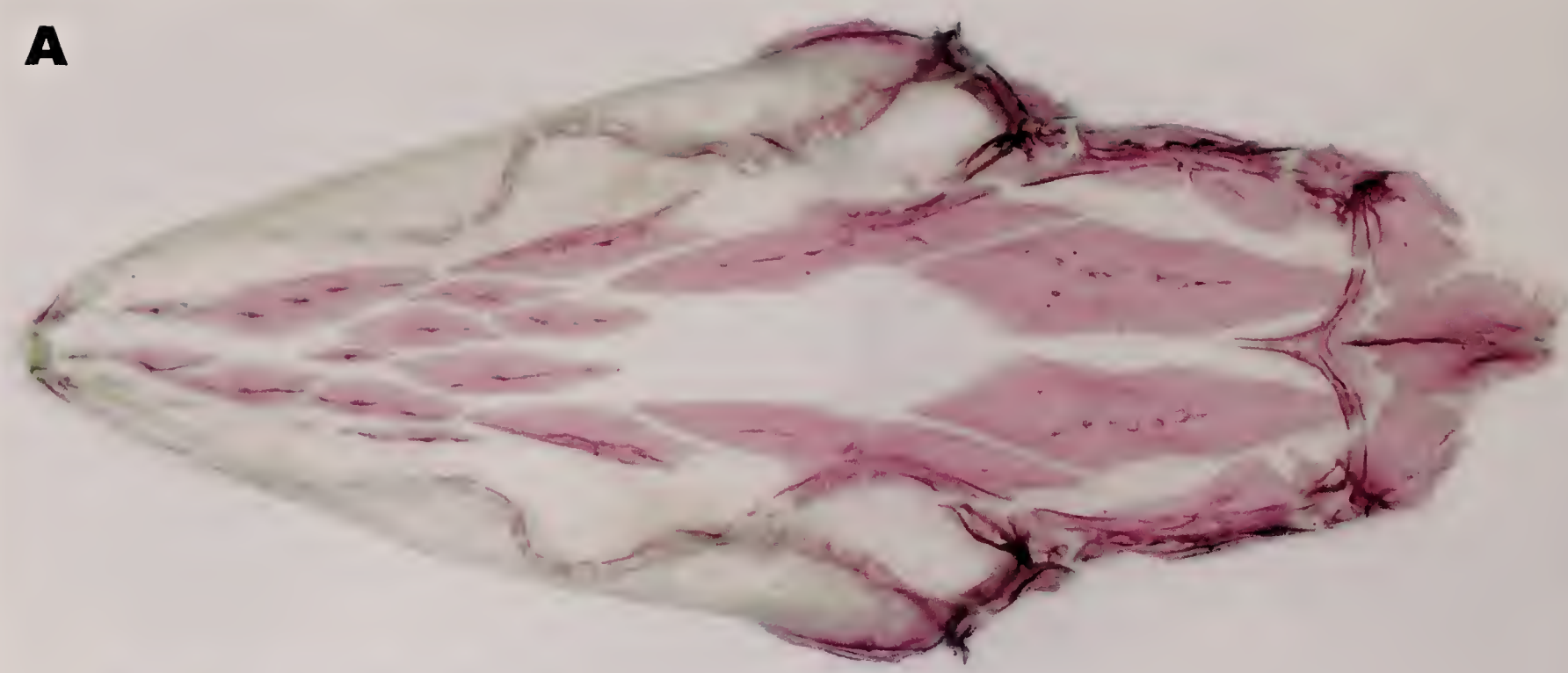


FIG. 17. *Acipenser brevirostrum*, skull roof of small juvenile showing early development, from VIMS 12080 (57.4 mm TL). (**A**) Photograph and (**B**) line drawing. Scale in millimeters. Anterior to left. Abbreviations found on pages 8–9.

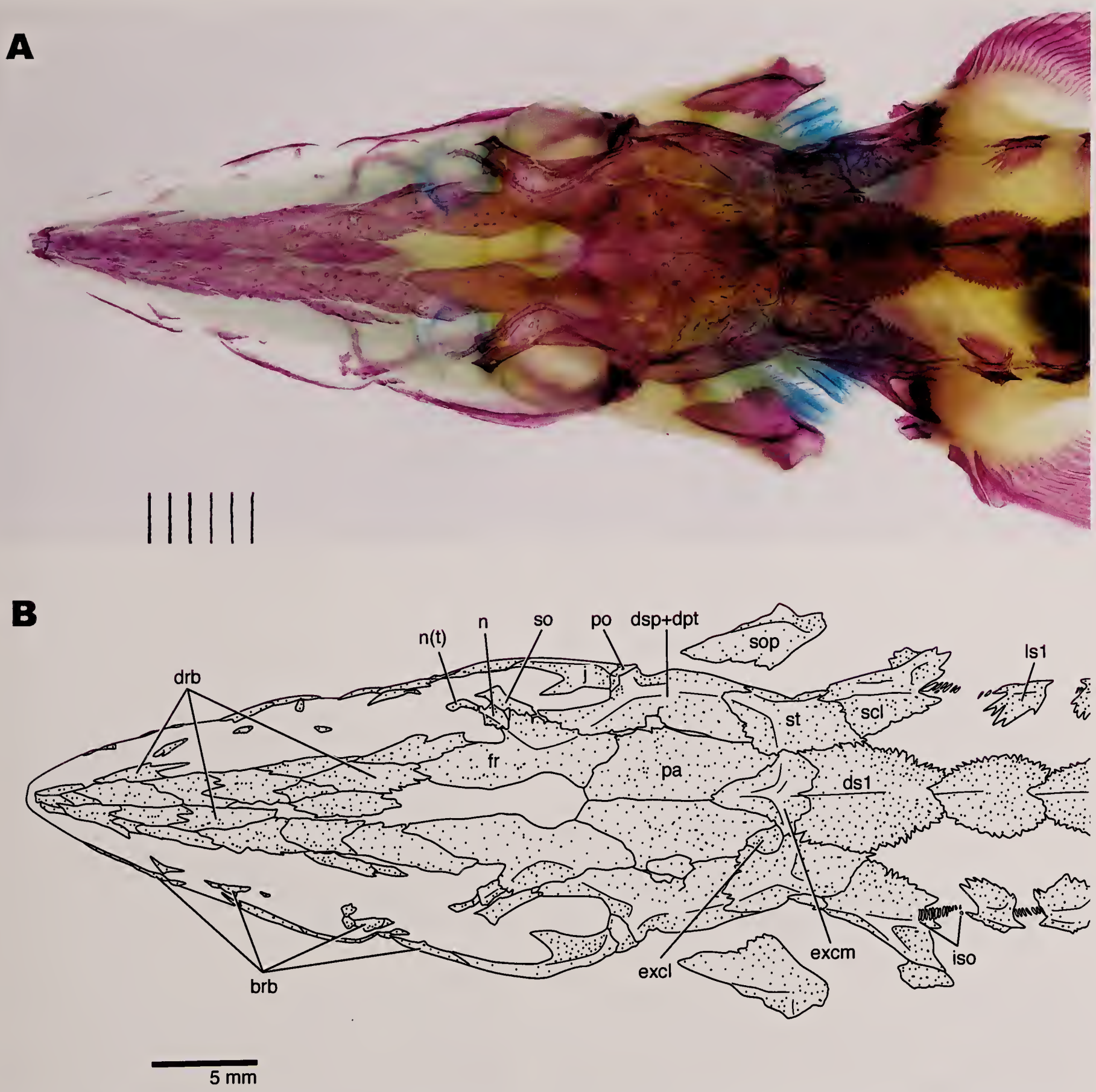


FIG. 18. *Acipenser brevirostrum*, skull and pectoral girdle of small juvenile showing early development of border rostral bones in dorsal view, from VIMS 12084 (127 mm SL). (**A**) Photograph and (**B**) line drawing. Scale in millimeters. Anterior to left. Abbreviations found on pages 8–9.

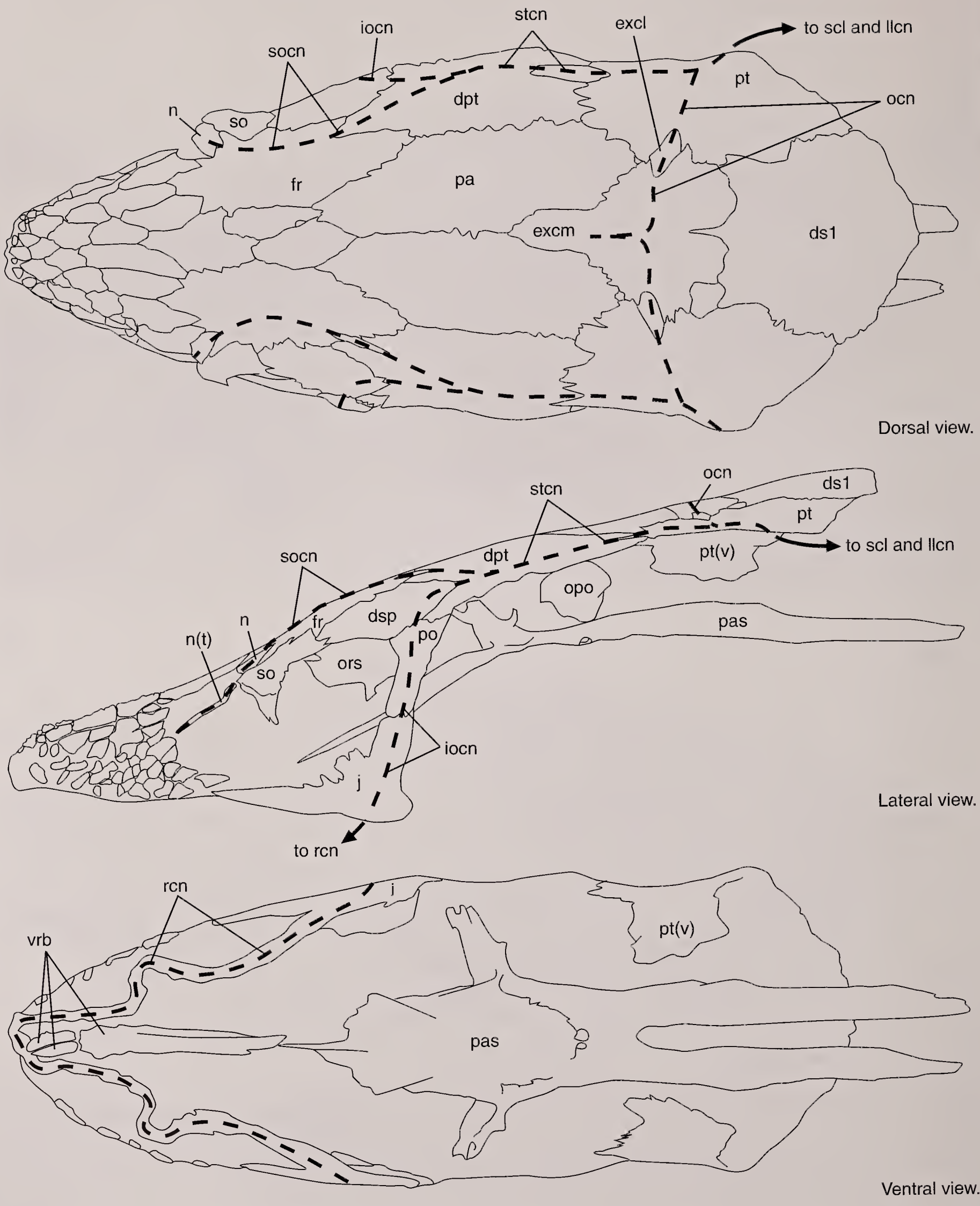


FIG. 19. *Acipenser brevirostrum*, major sensory canals and pit lines of the head in dorsal, lateral, and ventral views. Skull drawings are based on UMA F10431 (male, 930 mm SL). Canals are indicated by dashed line. Pathways of canals are based on study of cleared and stained specimens and tracing on adult dried skulls. Anterior to left. Abbreviations found on pages 8–9.

an elongate, unornamented posterior extension (**pap**, Fig. 12) that is overlapped by the dermopterotic, extrascapulars, and the first dorsal scute. This posterior extension forms much of the length of the parietal as a whole and may reach nearly the posterior margin of the posttemporals (Fig. 13). The dorsal surface of the parietal is also unornamented anteriorly (**paa**, Fig. 12) where it is overlapped by the anamestic bones positioned between the frontals. Hilton and Bemis (1999, table 4) found that the exposed portion of the parietal (equivalent to the ornamented surface) is individually and bilaterally variable in *A. brevirostrum* (see also Table 2).

Immediately anterior to the parietals are the frontals (**fr**, Figs. 8, 9, 11–18), which, like the parietals, are among the first bones of the skull roof to develop (noted in a 23.3 mm TL specimen) and first appear as thin splints of bone anterolateral to the "pineal" foramen. The frontals, which contact the parietals posteriorly and the dermopterotics, dermosphenotics, supraorbitals, and nasals laterally, vary greatly in size from individual to individual but overall are among the largest bones of the skull roof. The frontals have unornamented dorsal surfaces on almost every margin (Fig. 12), although this is most extensive anterolaterally and anteromedially. Medially and anteriorly, the frontals are surrounded by the anamestic bones of the snout (see below). Those anamestic bones that lie between the frontals were termed "pineal bones" by Findeis (1993; see below), but because of their extreme variation in size, position, and number and because they blend into other dorsal rostral bones, we do not consider them to be a distinct series. The typical condition for *A. brevirostrum* is to have the left and right frontals separated from one another by a variable number and pattern of such bones. In a few individuals, however, the frontals share a suture in the midline of the snout (e.g., Figs. 24A, E, 25A, E).

The dermosphenotic (**dsp**, Figs. 8, 9, 11–18) of *A. brevirostrum*, like that of other acipenserids, is fully incorporated into the skull roof. This bone, which is part of the infraorbital series and was found in a 23.2 mm TL specimen, is positioned dorsal to the posterior portion of the orbit and contacts the supraorbital anteriorly, the parietal and frontal medially, the dermopterotic posteriorly, and the postorbital posterolaterally. The lateral edge of the dermosphenotic is slightly curved, contributing to the smooth margin of the skull roofing bones above and behind the orbit.

The supraorbital of *A. brevirostrum* (**so**, Figs. 8, 9, 11–18) is a distinctively shaped anamestic bone that forms the anterodorsal margin of the orbit. This bone develops relatively late: we first observed it in a 51.6 mm TL specimen. A well-developed, ventrally directed process of the supraorbital typically is covered by skin and is unornamented. The supraorbital contacts the dermosphenotic posteriorly and the nasal and frontal medially. In all sturgeons except *Scaphirhynchus* (Findeis, 1997), there is typically a gap between the ventral process of the supraorbital and the jugal and posterior border rostral bones (e.g., Fig. 22). In one specimen of *A. brevirostrum* that we examined (FMNH 112214), the left supraorbital is greatly expanded ventrally so that it forms a broad suture with the posterior border rostral bones and forms a completely enclosed orbit; the right supraorbital of this specimen also nearly contacts the lateral rostral bones.

The anteriormost bone carrying the supraorbital sensory canal is the nasal, which is composed of two parts: 1) a posterior ornamented nasal (**n**, Figs. 8, 9, 11–18) and 2) an anterior series of tubular bones (**n(t)**) that surround the supraorbital canal as it bends ventrally between the incurrent and excurrent nasal openings (Figs. 15–19, 23). Both portions of the nasal were found in specimens 51.6 mm TL and longer. The ornamented portion of the nasal is consistently present as a single element (one on each side), although its exact shape is variable, ranging from triangular to oval; it is infrequently fused to the frontal. This element contacts the frontal and supraorbital posteriorly and variably contacts bones of the anamestic rostral series, from which it may be difficult to distinguish if the sensory canal is obscured. The tubular portion of the nasal consists of irregularly shaped tubes of bone that vary in shape and number.

Two bones form the posterior margin of the orbit. The dorsal of these, the postorbital (**po**, Figs. 15–19, 26, 27, 35–37), receives the infraorbital canal from the dermosphenotic and was observed in specimens larger than 42.3 mm TL. The anterior margin of the postorbital is slightly concave so that the posterior rim of the orbit is smoothly curved. The more ventral of the postorbital bones is the jugal (**j**, Figs. 15–19, 26, 27, 35–37), which completes the infraorbital series of bones (the canal and its ossicles continue anteriorly as the rostral sensory canal and bones; see the section Braincase; see also Hilton, 2002a). The jugal is present in a 21.9 mm TL specimen as a small ossification surrounding the infraorbital sensory canal at the ventralmost part of the canal (i.e., where it bends medially as the rostrosensory canal). In the adult, in medial view, there are definite horizontal and vertical axes of the jugal of *A. brevirostrum* that form a right angle and a backward-L shape (Fig. 44). In lateral view, however, the ornamented portion of the jugal grows to "fill in" the L to form a roughly triangular-shaped element (Fig. 43). A similar condition is also found in *A. fulvescens*. This differs from that of other species of *Acipenser* (e.g., *A. oxyrinchus*), in which the horizontal and vertical axes of the jugal remain distinct in lateral view (see Hilton, 2002a, fig. 2).

Anamestic Bones of the Dorsal Rostrum

The snout of *A. brevirostrum*, as in all other acipenserids, is armored by irregularly shaped and positioned anamestic bones. We recognize two series of bones covering the snout, following, in part, Findeis (1993), who distinguished between those bones that form the dorsal surface of the snout—the dorsal rostral bones (**drb**, Figs. 8, 9, 15–18, 26, 27)—and those that form posteroventrally to the ampullary fenestrae—the border rostral bones (**brb**, Figs. 26, 27). Findeis (1993) distinguished the posterior three or four border rostral bones from the more anterior ones, which he termed the lateral rostral bones. We regard them all as a single series, as we did not observe the differences in the "structure, consistency, and separate ontogeny" of the two series cited by Findeis (1993, p. 115; also, a few lines above, he noted, "Ontogenetically, these [the border rostral bones] develop simultaneously with the lateral rostral bones"). The dorsal rostral bones were first observed in a 42.3 mm TL specimen.

Not much can be said regarding the shape of either the dorsal or the border rostral bones, as they are randomly arranged on the snout as "space filling bones" (Westoll, 1936), and there is no correspondence of individual elements between different specimens of the same species (see Hilton & Bemis, 1999). Even so, the form of the individual border rostral bones or dorsal rostral bones as a distinct series is phylogenetically

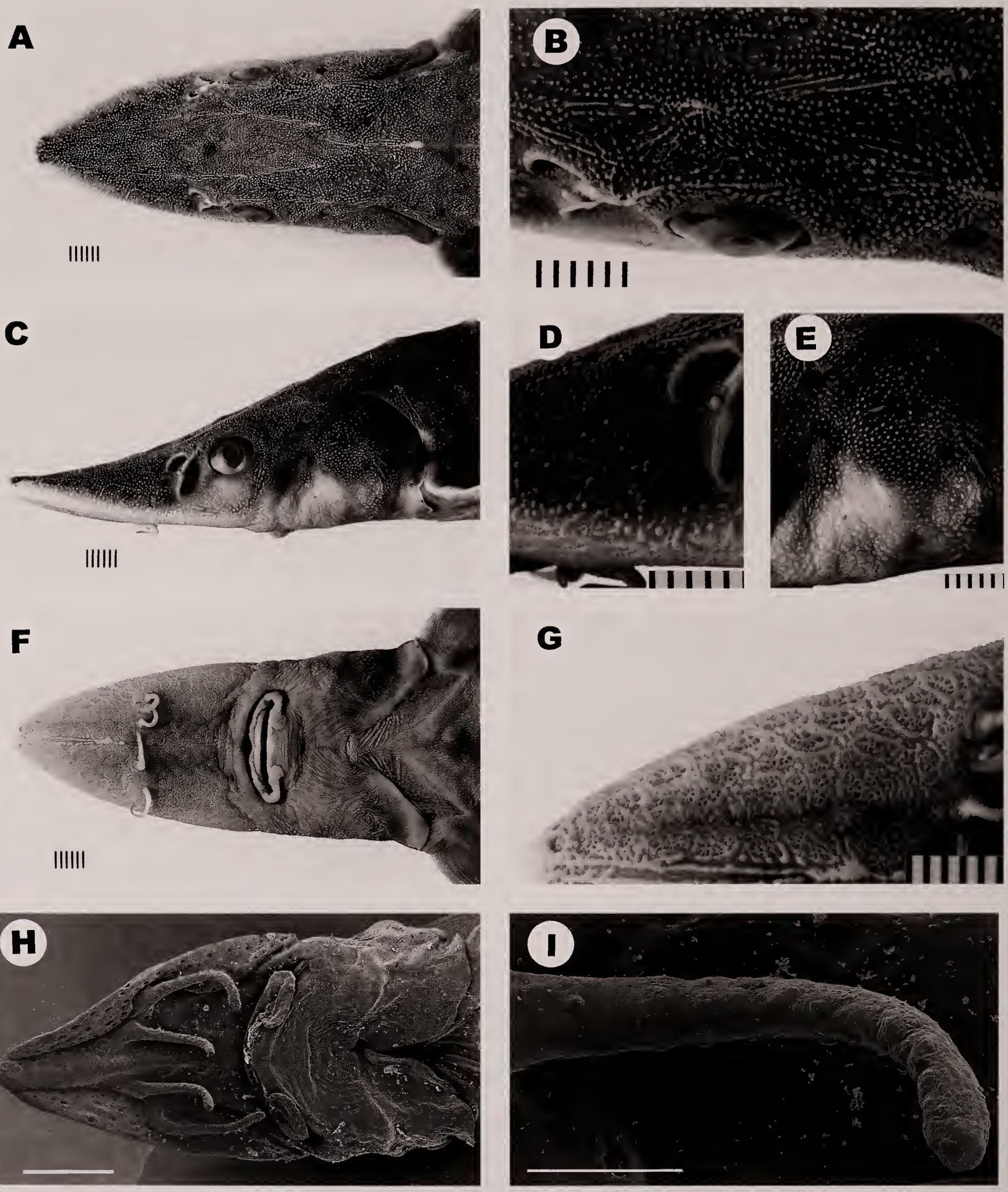


FIG. 20. *Acipenser brevirostrum*, photographs showing distribution of ampullary organ fields on head. (**A**) Head in dorsal view. (**B**) Close-up of supraorbital ampullary field. (**C**) Head in lateral view. (**D**) Close-up of posterior portion of dorsal rostral field. (**E**) Close-up of opercular ampullary field. (**F**) Ventral view of head. (**G**) Close-up of left anterior portion of ventral rostral ampullary field. (**H**) Scanning electron micrograph of small individual showing development of rostral sensory canal as a groove on the ventral surface of snout and eruption of ampullary organs. (**I**) Close-up of inner right barbel showing covering of taste buds. (**A–G**) VIMS 11614, 255 mm SL, scale in millimeters. (**H, I**) VIMS 12085, est. 18.5 mm TL; scale = 1 mm and 0.5 mm, respectively.

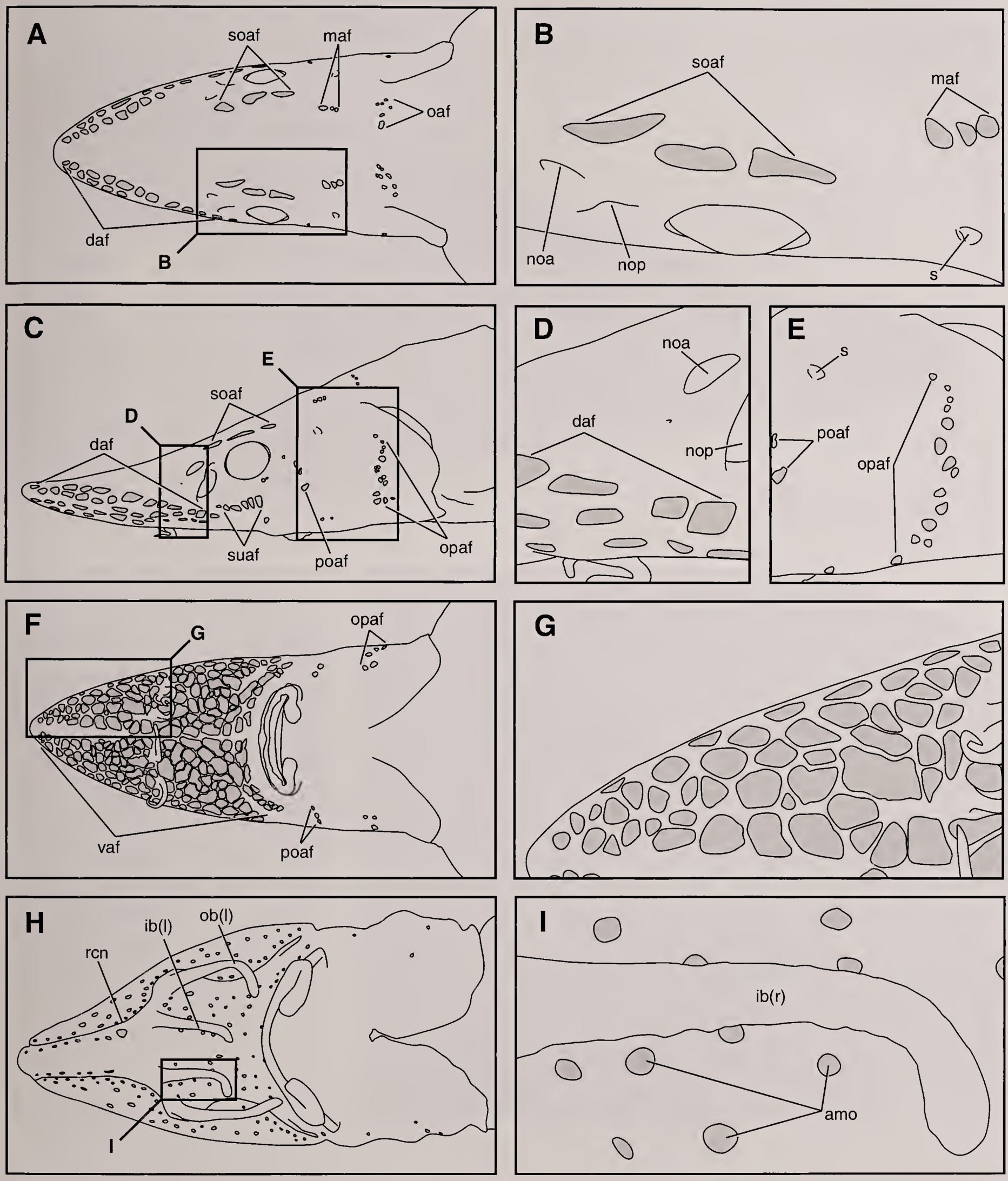


FIG. 21. Schematic line drawings of Figure 20. Gray indicates ampullary organ rosettes. Abbreviations found on pages 8–9.

FIG. 22. *Acipenser brevirostrum*, cleared and stained head of small adult specimen, from MCZ 54167 (sex unknown, 472 mm SL). (**A**) Whole head in lateral view, showing bones of head and small dermal plates embedded in the skin (stained red). (**B**) Close-up of nares and orbital region showing sclerotic bones (large black arrowheads) and pores from tubular nasal sensory canal bones (small white arrowheads). (**C**) Ossicles of the preopercular sensory canal (small black arrowheads). Anterior to left in all. Scale bar in **A** = 2 cm; in **B** and **C**, scale in millimeters. Abbreviations found on pages 8–9.

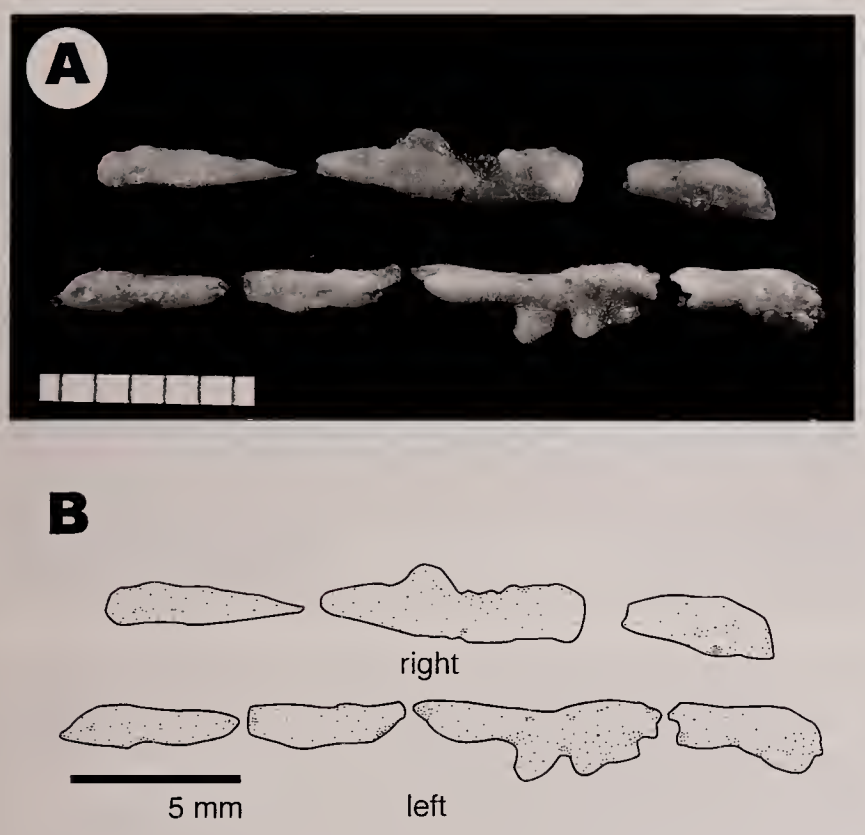


FIG. 23. *Acipenser brevirostrum*, tubular nasal bones in dorsolateral view, from UMA F10547 (male, 915 mm SL). (**A**) Photograph and (**B**) line drawing. Note that these elements are individually variable in shape and number. Anterior to left.

variable (see the section Phylogenetic Analysis, character 12). The dorsal rostral bones are irregular in shape, and in *A. brevirostrum* they are relatively short, block-like bones that blend seamlessly into the border rostral bones. They tend to be smaller toward the tip of the snout, where they become embedded in the much thicker dermis of that region.

Findeis (1993) recognized a distinct subseries of the dorsal rostral bones, the so-called pineal bones, which form between the anterior portions of the left and right frontals. These elements are variable in presence, number, and shape; their correspondence between specimens is doubtful. Findeis (1997, character 32) used the presence of this series as a character of his Acipenserinae (i.e., there is a pineal fontanelle in this region in polyodontids and *H. huso*, Findeis, 1997, fig. 18a and b, although in adult specimens of *Huso*, the fontanelle may be closed by the frontals coming into contact along the midline; see Kittary, 1850, pl. 7, fig. 1; this fontanelle may also be present in some species of *Acipenser*, e.g., *A. oxyrinchus*; Hilton, pers. obs.).

The dorsal rostral bones of sturgeons are likely homologous as a series to the dorsorostral bones of polyodontids (termed a, b, and c bones by Bridge, 1878; Grande & Bemis, 1991; Grande et al., 2002), although there is no recognizable pattern to them, as there is, for example, in *Polyodon* (Grande & Bemis, 1991, fig. 6). We note that in the primitive polyodontid †*Protopsephurus*, the a, b, and c bones are more "sturgeon-like" than in other polyodontids (Grande et al., 2002, figs. 7, 8).

In general, the border rostral bones are confined to the dorsolateral edges of the snout, although in a few specimens we found well-developed border rostral bones on the ventrolateral surface of the snout (e.g., MCZ 54167; this is one reason we term them "border" rather than "lateral" rostral bones; i.e., they are not necessarily restricted to the lateral margin of the snout). It is interesting to note that in individuals such as this, the ventral border rostral bones bear a superficial resemblance to the stellate bones of paddlefishes, albeit smaller than and not as slender as those found, for instance, in *Polyodon*. The border rostral bones develop much later in ontogeny than do the dorsal rostral bones (first observed in a 96 mm TL specimen; see also Findeis, 1993), although there is no obvious ontogenetic pattern (from individual to individual) in the dorsal rostral bones of *A. brevirostrum*. For instance, while still rudimentary in their development (onset of development begins at 50.4 mm TL), those of a 51.6 mm TL specimen were found to be much more robust than those of a 58.7 mm TL specimen.

Braincase

Our use of the term "braincase" follows Grande and Bemis (1998) in referring to the endoskeleton of the skull (= cartilage and ossified portions of the neurocranium) and its dermal sheathing bones (i.e., the parasphenoid and ventral rostral bones in sturgeons). The braincase of different species of *Acipenser* has previously been described and illustrated by Kittary (1850; Caspian Sea species), Stensiö (1932, figs. 34, 35; *A. sturio*), Holmgren and Stensiö (1936, figs. 334, 335, 336; *A. gueldenstaedti*), and Hilton and Bemis (1999, figs. 11, 13; *A. brevirostrum*). In his description of the chondrocranium, Kittary (1850) named and described 14 regions of the braincase of acipenserids, based on the relationship with overlying dermal bones. The terminology of Findeis (1993), who recognized five regions of the chondrocranium in his description of *Scaphirhynchus*, is also usefully applied to other acipenserids and will be followed here with only slight modification. Anterior to posterior, the regions of the braincase include the rostroethmoid region (rostrum and ethmoid regions of Findeis, 1993), the orbital region, the otic region, and the occipital region (occipital and vertebral regions of Findeis, 1993).

The chondrocranium is extensive in *A. brevirostrum*, as in all acipenserids (e.g., see Findeis, 1993, for *Scaphirhynchus*). Although the chondrocranium is largely unossified, several centers of perichondral ossification are relatively stable in their position on the neurocranium (Figs. 29–33, 40, 41), although their shape and presence is highly variable (Hilton & Bemis, 1999). Similar to Findeis (1993), we discovered that the perichondral bones of the braincase may completely line the foramina within an individual element and may even follow the foramen into the internal chamber of the braincase. However, we never observed any trace of endochondral ossification in any of our specimens. The ossifications of the neurocranium that have been identified in *A. brevirostrum* include the epioccipital, exoccipital, opisthotic, prootic, orbitosphenoid, and the lateral ethmoid. All these bones are generally paired.

We made only limited observations on the development of the braincase; most of the early chondrifications had already occurred in our earliest cleared and stained stages, and the chondrocranium was a single unit in our smallest specimens. The synotic tectum already is complete by 18.8 mm TL, separating the anterior and posterior fontanelles on the dorsal surface of the chondrocranium. Information on the early development of the braincase in sturgeons can be found in Parker (1882), Sewertzoff (1928), de Beer (1925, 1937), and Holmgren and Stensiö (1936); this will be the focus of a future study using our newly collected specimens. Here we emphasize the general anatomy of the braincase and its relationship to the skull roof and other portions of the skull.

In the smallest specimens, there is a large foramen anterior to the anterior fontanelle, defined posteriorly by the

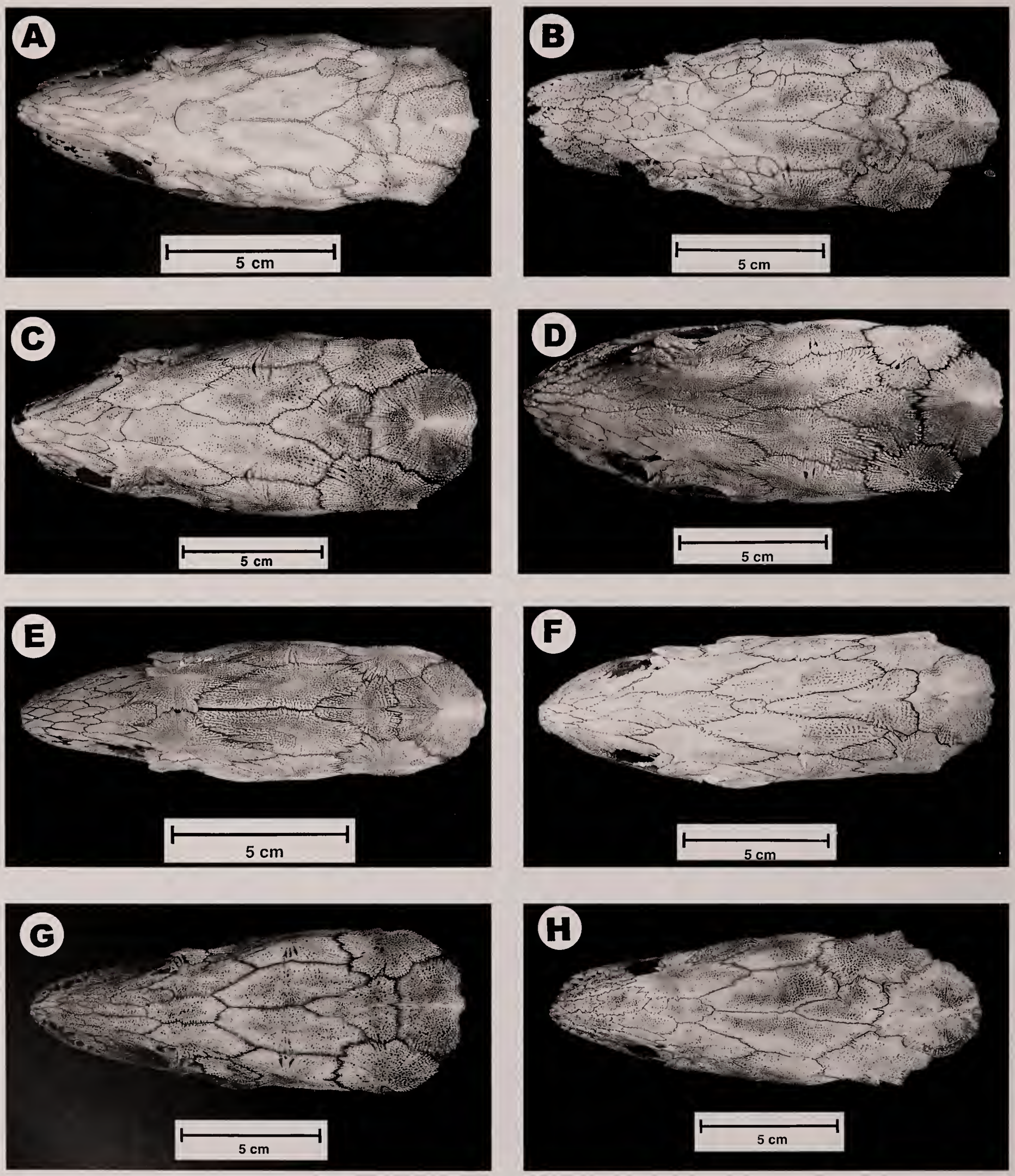


FIG. 24. *Acipenser brevirostrum*, dermal bones of the skull roof showing variation in pattern of ossifications. (**A**) UMA F10016 (sex unknown, 600 mm SL). (**B**) UMA F10521 (male, 640 mm SL). (**C**) FMNH 112214 (sex unknown, 763 mm SL). (**D**) UMA F10018 (male, 725 mm SL). (**E**) FMNH 112213 (sex unknown, 630 mm SL). (**F**) FMNH 112211 (sex unknown, 537 mm SL). (**G**) VIMS 12073 (female, 660 mm SL). (**H**) VIMS 12071 (male, 705 mm SL). Anterior to left.

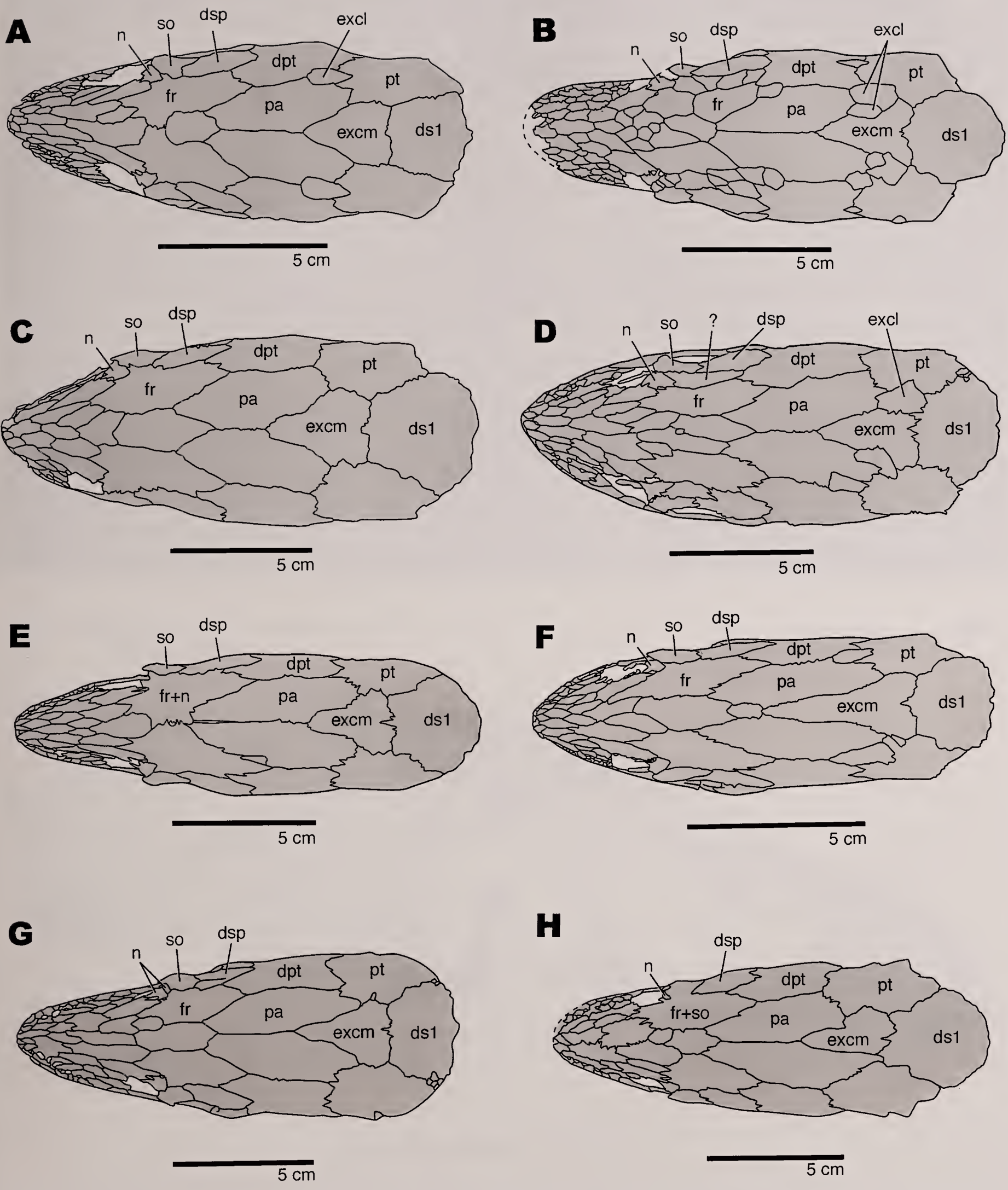
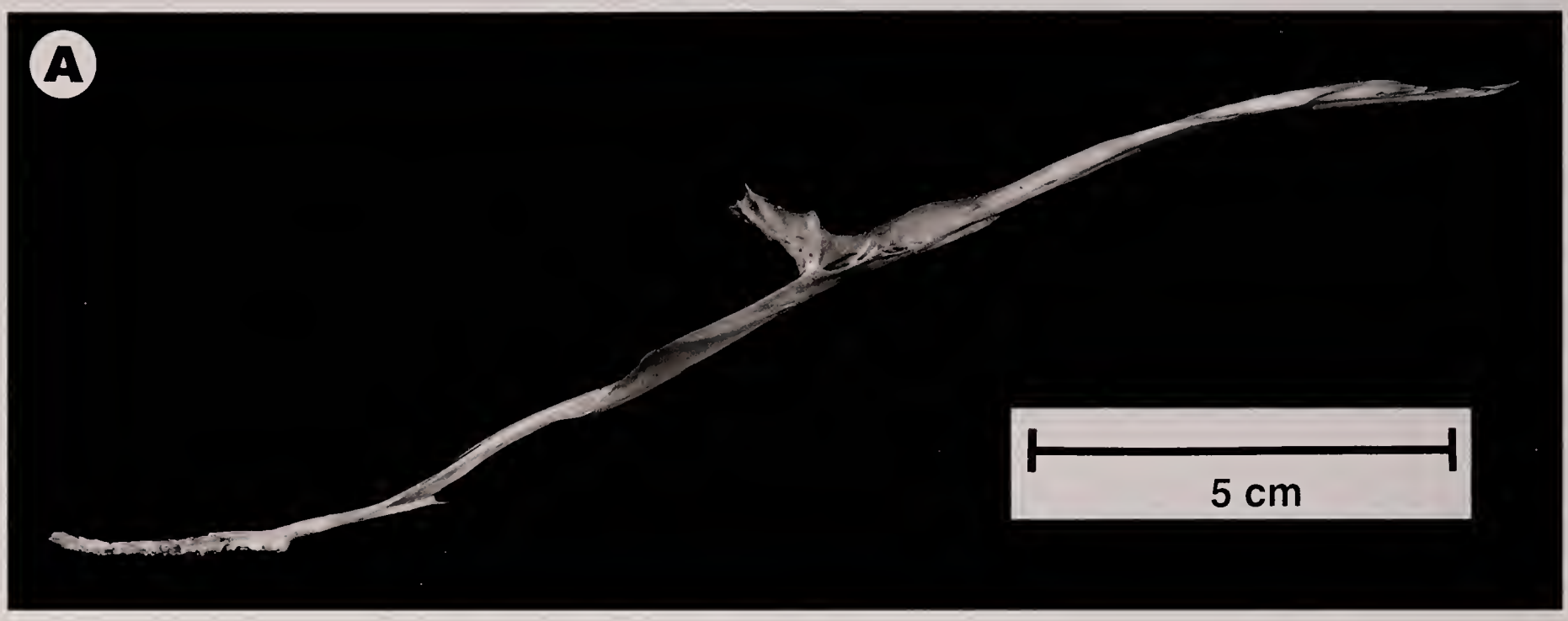


FIG. 25. *Acipenser brevirostrum*, dermal bones of the skull roof showing variation in pattern of ossifications; line drawings of Figure 24. Abbreviations found on pages 8–9.

FIG. 26. *Acipenser brevirostrum*, skull and pectoral girdle of adult in lateral view, from FMNH 112212 (sex unknown, 710 mm SL). (**A**) Photograph and (**B**) line drawing. Slight distortion of specimen due to displacement of elements during drying (particularly evident on the anterior portion of the ventral snout). Branchial arches removed from specimen. Most soft tissue and cartilage present on this specimen have been omitted from the line drawing. Anterior to left. Abbreviations found on pages 8–9.

FIG. 27. *Acipenser brevirostrum*, dermal bones of the skull roof and portions of the neurocranium in lateral view, from UMA F10431 (male, 930 mm SL). **(A)** Photograph and **(B)** line drawing. Dashed line on lateral ethmoid and parasphenoid indicate portions of these bones obscured in the photograph by cartilage. Most soft tissue and all cartilage present on this specimen have been omitted from the line drawing. Anterior to left. Abbreviations found on pages 8–9.



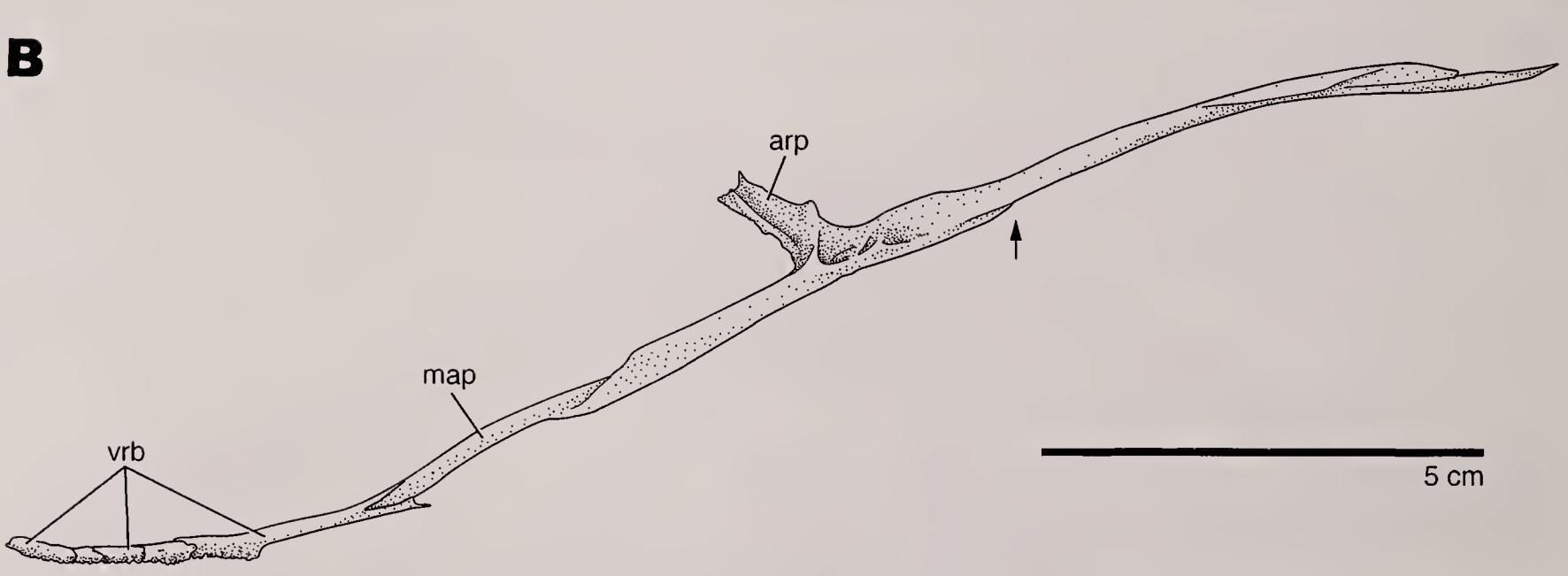


FIG. 28. *Acipenser brevirostrum*, parasphenoid and ventral rostral bones in lateral view, from VIMS 12074 (female, 695 mm SL). (**A**) Photograph and (**B**) line drawing. Arrow indicates anterior extent of aortic notch. Anterior to left. Abbreviations found on pages 8–9.

FIG. 29. *Acipenser brevirostrum*, neurocranium in lateral view, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing. In photo, bone is stained red, and cartilage appears white; in drawing, bone is white, and cartilage is gray. Anterior to left. Abbreviations found on pages 8–9.

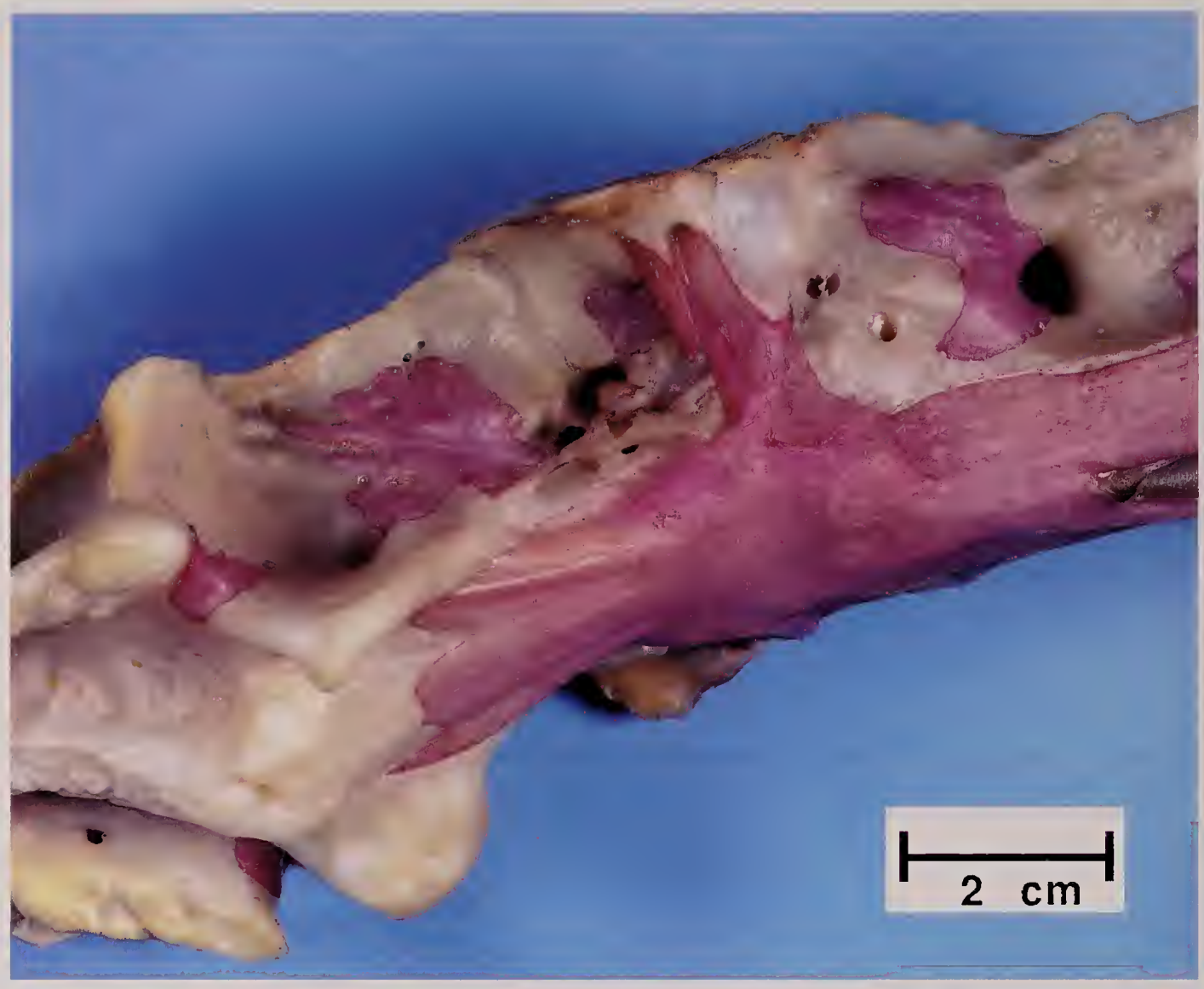


FIG. 30. *Acipenser brevirostrum*, left orbital region of neurocranium in oblique ventrolateral view, from FMNH 113538 (female, 960 mm SL). Bone is stained red, and cartilage appears white. Anterior to left.

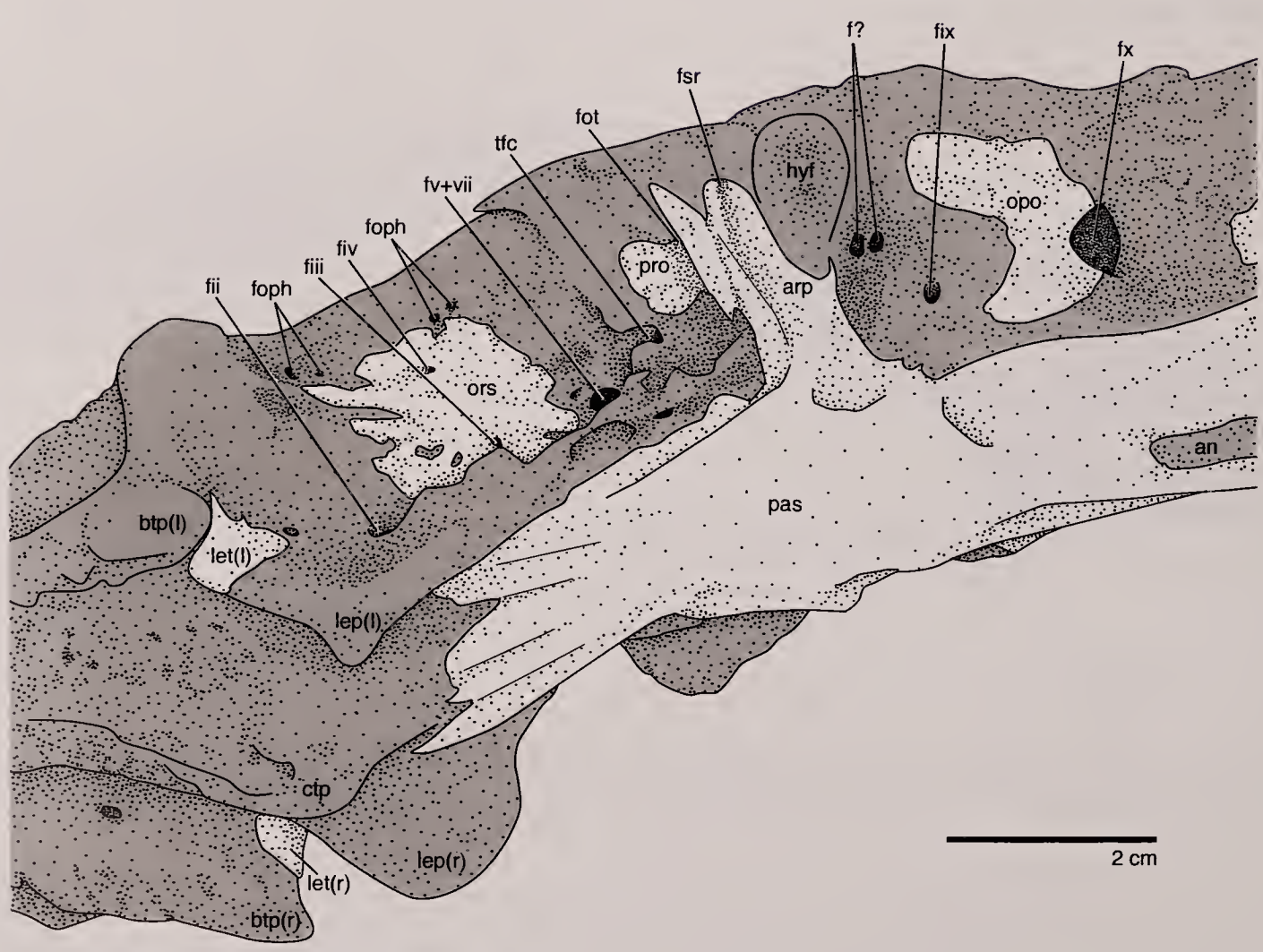


FIG. 31. *Acipenser brevirostrum*, left orbital region of neurocranium in oblique ventrolateral view. Line drawing of Figure 30. Abbreviations found on pages 8–9.

FIG. 32. *Acipenser brevirostrum*, right orbital region of neurocranium in oblique ventrolateral view, from FMNH 113538 (female, 960 mm SL). Bone is stained red, and cartilage appears white. Anterior to right.

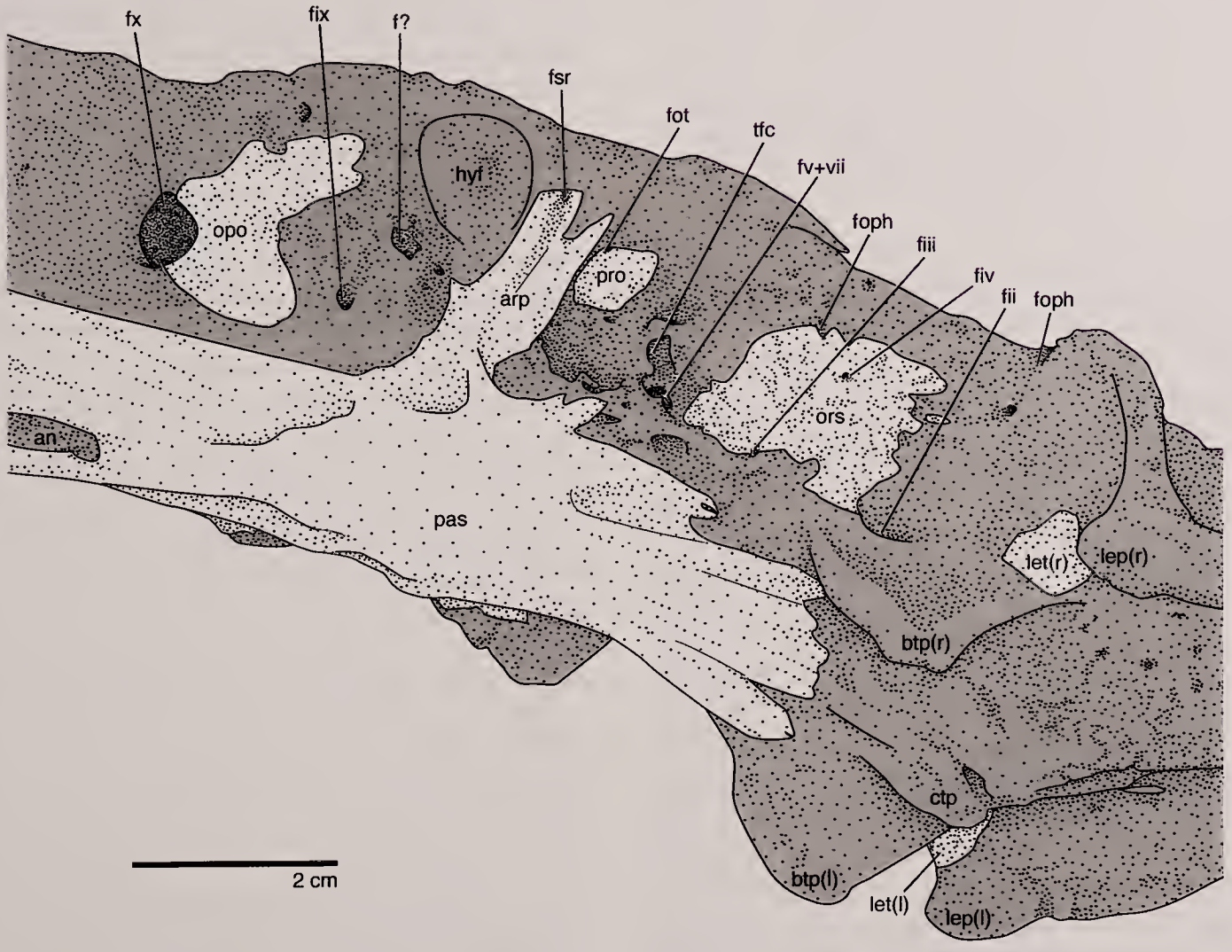


FIG. 33. *Acipenser brevirostrum*, left orbital region of neurocranium in oblique ventrolateral view. Line drawing of Figure 32. Abbreviations found on pages 8–9.

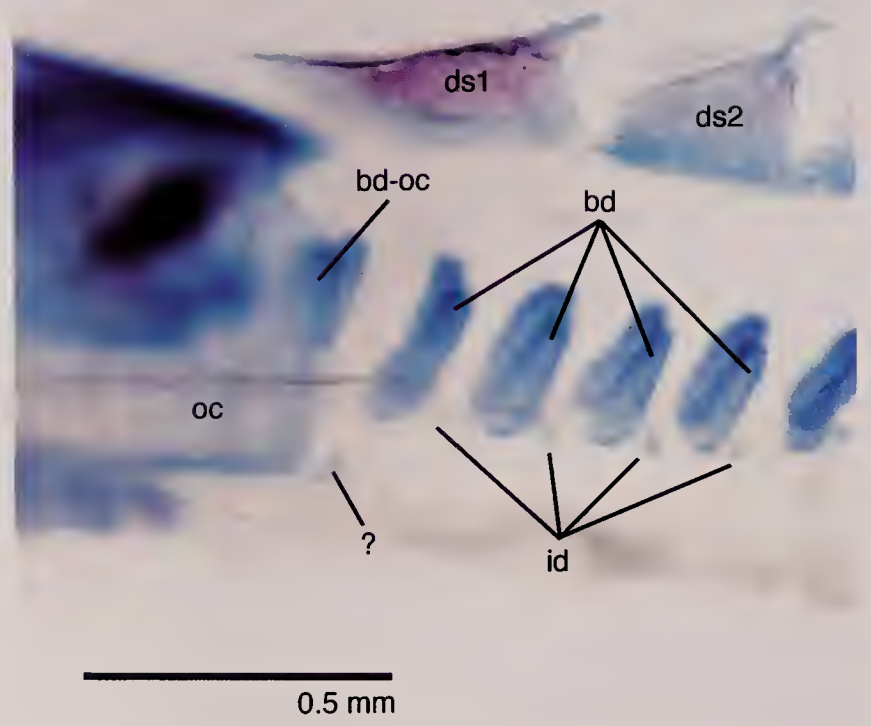


FIG. 34. *Acipenser brevirostrum*, occipital region at early stage of development, from VIMS 12076 (22.1 mm TL). Abbreviations found on pages 8-9.

epiphysial bridge (Fig. 16A). The cartilage of the chondrocranium grows to completely fill the anterior and posterior fontanelles in *A. brevirostrum*; the anterior fontanelle is completely filled by 21.0 mm TL and the posterior fontanelle by 27.6 mm TL (the cartilage in the region of the posterior fontanelle may be thin and easily broken in the adult; e.g., Hilton & Bemis, 1999, fig. 11A). In other species of *Acipenser* (e.g., *A. transmontanus*, pers. obs.), the posterior fontanelle persists into the adult; the chondrocranium of *Scaphirhynchus* has a solid roof, as does *A. brevirostrum* (Findeis, 1993).

The rostroethmoid region of the neurocranium, which extends from the tip of the snout posterior to the level of the postnasal wall (**pnw**, Fig. 29), undergoes dramatic ontogenetic change in its overall shape in *A. brevirostrum*, from being anteriorly pointed in larvae and small juveniles (e.g., Figs. 15, 16, 42C, D) to a bluntly rounded anterior end in the adult (e.g., Fig. 10). The dorsal surface of the rostroethmoid region is covered by an array of grooves marking the course of blood vessels and nerves lying beneath the dermal bones of the snout. The dominant feature of this portion of the skull is the pair of nasal capsules, which are deep, rounded sulci (**ncap**, Figs. 10, 29). The ventral surface of the rostroethmoid region is marked by a pair of deep grooves that parallel the midline of the snout (Fig. 41). These grooves are filled largely with adipose tissue, though they also house the nerves supplying the chemosensory barbels and the ampullary organs that cover the ventral surface of the snout (Findeis, 1993). Along the midline of the rostroethmoid region is a well-developed ridge that terminates posteriorly at the so-called central trabecular process (**ctp**, Figs. 29–33, 41). The lateral ethmoid (**let**, Figs. 29, 30–33, 41) is the only ossification of the rostroethmoid region and is confined to the posteriormost part of this region. This bone forms around the ventral angle of the postnasal wall between the basitrabecular and lateral ethmoid processes (**btp**, **lep**, Figs. 29, 30–33, 41) and may extend relatively far anteriorly along the ventral surface of the rostrum on the floor of the deep grooves in the cartilage (see Hilton & Bemis, 1999, fig. 11). Dorsally, the lateral ethmoid is pierced by the formen for the olfactory nerve.

The orbital region of the braincase is defined anteriorly by the postnasal wall and posteriorly by the ascending rami of the parasphenoid. The left and right orbits are deeply excavated, and a large foramen for the optic nerve is positioned more or less in the middle of this concavity. The dorsal margin of the orbit forms a notch in the neurocranium in dorsal view (Fig. 10). Posterior to the orbit itself is a broad yet thin roofing cartilage, the orbital shelf (**os**, Fig. 10), that is tightly associated with the dermosphenotic and the dermopterotic. The braincase is widest at the level of this orbital shelf. The only perichondral ossification of the orbital region we found in *A. brevirostrum* is the orbitosphenoid (**ors**, Figs. 27, 29, 30–33), which is also the largest of the ossifications typically found in the adult neurocranium, although there is great variation (including bilateral asymmetry) in the shape and size of this bone, as there is also in the pattern of foramina in this region (cf. Figs. 30–33). The orbitosphenoid forms around the posterior margin of the optic nerve foramen and may grow posteriorly to contact the anterior portion of the trigeminofacialis chamber. The orbitosphenoid also typically surrounds the occulomotor and trochlear nerve foraminae.

The left and right portions of the otic region of the braincase are the first parts of the braincase to develop as cartilage (present in 15.0 mm TL specimens). These cartilages grow anteriorly as parachordal cartilages to form the floor of the orbital region and dorsally to surround the semicircular canals of the inner ear. The otic region, demarcated anteriorly by the ascending processes of the parasphenoid, is marked laterally by a deep facet for articulation of the hyomandibula (**hyf**, Figs. 29, 30–33). The suprapharyngobranchials (**spb**, Figs. 73, 74) also articulate with the braincase in the otic region (spb1 in a shallow depression posteroventral to the hyomandibular facet and spb2 posterior to the foramen for the vagus nerve). In the adult, the positions of the anterior and posterior semicircular ducts are indicated by distinct depressions on the dorsal surface of the braincase (Fig. 10). Two ossifications form in the otic region of the braincase. The more posterior of these is the opisthotic (**opo**, Figs. 26, 29–33, 38, 39, 41), which is associated with the anterior margin of the large foramen for the vagus nerve (**fx**, Figs. 30–33). The anterior extent of the opisthotic is variable, but it may grow to contact the foramen for the glossopharyngeal nerve (**fix**, Figs. 30–33). The other ossification of the otic region is the prootic (**pro**, Figs. 30–33). The prootic lies anterior to the ascending process of the parasphenoid (and in some cases deep to the ascending process of the parasphenoid) and is generally visible only in ventral view. In many specimens, the prootic is continuous with bone on the dorsal surface of the neurocranium (see Hilton & Bemis, 1999, fig. 11; = alisphenoid of Holmgren & Stensiö, 1936), which is best regarded as a dorsal portion of the prootic. The dorsal (if developed) and ventral portions of the prootic are connected through a foramen for the otic ramus of the facial nerve (Marinelli & Strenger, 1973).

In the midline, the neurocranium is drawn out posteriorly. Posterolaterally, there are exaggerated posttemporal processes (**ptp**, Figs. 19, 29, 40, 41) that are tightly associated with the medial surfaces of the ventral processes of the posttemporals.

These lateral processes and the median crest define the left and right posttemporal fossae (**ptf**, Figs. 10, 40), which receive the epaxial body musculature. The lack of distinction between the occipital region of the skull and the vertebral column in acipenserids has been commented on by many authors (e.g., Shute, 1972; Findeis, 1993; Bemis & Forey, 2001). The posterior extent of the occipital region is difficult to determine because up to five anterior vertebral segments are incorporated into the skull of the adult (Figs. 29, 34). See Bemis and Forey (2001) and Britz and Johnson (2010) for discussion of the posterior limits of the braincase in actinopterygian fishes, with a discussion of sturgeons in particular. Two pairs of bones are typically found in the occipital region of *A. brevirostrum*. The epioccipitals (**epo**, Figs. 10, 29, 40) are the dorsolateralmost ossifications of the occipital region of the skull and in many specimens are continuous with the exoccipitals (e.g., Hilton & Bemis, 1999, fig. 13); the left and right epioccipitals may fuse across the dorsal midline of the braincase. The exoccipitals (**exo**, Figs. 10, 29, 40, 41; = pterotic of Findeis, 1993, fig. 47) develop on the ventral surface of the occipital region and surround the foramina for the anterior spino-occipital nerves. As with the epioccipitals, the exoccipitals are extremely variable in their form and may be extensive (Hilton & Bemis, 1999, fig. 13). In some specimens (e.g., UMA F10578, 899 mm SL; FMNH 113538, 960 mm SL), the exoccipitals, epioccipitals, and the ossified portions of the anterior vertebrae are completely fused and continuous with one another, making it impossible to determine the limits of any one of the ossifications (these were among the largest specimens examined, but others of similar sizes did not show such fusions, e.g., VIMS 12072, 940 mm SL). In contrast to Patterson (1975, p. 464), we never found the exoccipitals of *A. brevirostrum* to "ossify through-out the thickness of the cranial cartilage"; rather, they were found to be formed only by perichondral bone, as are all chondral bones of sturgeons (as noted, perichondral ossification of the chondrocranium may follow foramina and therefore may be on both the external and the internal surfaces of the cartilage).

The dermal bones on the ventral surface of the neurocranium and rostrum of *A. brevirostrum*, as for other acipenserids, consist of the parasphenoid, the ventral rostral bones, and the rostral canal bones. The rostral canal bones (**rcb**, Figs, 17, 26, 38, 39, 42–44) of *A. brevirostrum* were illustrated and described by Hilton (2002a). As in all acipenserids, the rostral canal bones are irregular gutter-like or tubular bones that develop in association with the rostral sensory canal, which is the anterior extension of the infraorbital sensory canal (see the section Sensory Canals, Ampullary Organs, and Sclerotic Capsule). As a series, these bones first appear at 26.2 mm TL as tiny specks of bone associated with the rostral sensory canal (although the jugal and lateral canal bones appear slightly earlier). The posterior elements in this series interdigitate with one another anteriorly and posteriorly, and the posteriormost element is closely associated with the medial flange of the jugal (Fig. 38). The more anterior elements in this chain of bones are tubular and may not contact other elements in the series. As discussed by Hilton (2002a), the Y-shaped elements that lie lateral to the anterior commissure between the left and right rostral sensory canals have been interpreted as antorbital bones by some workers (e.g., Allis, 1905), although such homology is difficult to establish. Therefore, we follow Hilton (2002a) by calling this bone the lateral rostral canal bone (see also Jollie, 1969).

The parasphenoid (**pas**, Figs. 27–33, 41–46) of *A. brevirostrum* is the largest bone of the ventral cranial skeleton and sheathes much of the ventral surface of the neurocranium; the smallest specimen observed with an ossified parasphenoid was 42.3 mm TL. The posterior portion of the parasphenoid has two elongate processes that extend far back to underlie the occipital region of the neurocranium and the anterior vertebral elements. These processes directly support up to five pairs of ribs (those of the vertebrae that have been incorporated into the neurocranium and other anterior vertebrae) and form a deep aortic notch; this posterior elongation is the typical condition for Acipenseriformes (e.g., Grande & Bemis, 1991, 1996; Bemis et al., 1997; Grande et al., 2002; Grande & Hilton, 2006). The main body of the parasphenoid typically supports a pair of foraminae for the efferent branchial arteries (Findeis, 1993), although there is much individual variation in their position and presence (i.e., in some individuals, one or both foraminae are represented by notches that are continuous with the anterior limits of the aortic notch; Figs. 45, 46). The deeply grooved ascending rami of the parasphenoid (**arp**, Figs. 26–33, 39, 40–46) extend from the lateral margin of the parasphenoid anteriorly lining the otic region of the neurocranium anterior to the articular facet for the hyomandibula. This is the same in all sturgeons examined here, except for †*Priscosturion*, in which the ascending processes extend posteriorly from the body of the parasphenoid (Grande & Hilton, 2006, fig. 18).

The anterior margin of the parasphenoid forms a median anterior process (**map**, Figs. 26, 28, 38, 39, 43–46) that is partially embedded in the cartilage of the neurocranium. A similar process is found in all other acipenserids (e.g., see Findeis, 1993, for *Scaphirhynchus* and Sewertzoff, 1926c, for *Pseudoscaphirhynchus*) as well as in the polyodontid †*Protopsephurus* (Grande et al., 2002, fig. 7; most polyodontids do not have an anterior process of the parasphenoid). Findeis (1993, fig. 56) discussed the acipenseriform parasphenoid, with particular regard to the presence of an anterior process as a synapomorphy of Acipenseridae + Polyodontidae (although it was not included as a character in his 1997 analysis). Findeis (1993) noted that the anterior part of the parasphenoid in *Huso* and †*Paleosephurus* tapers rather than forming a distinct process that meets the ventral rostral bones. In polyodontids (except for †*Protopsephurus*), there is no distinct process, and the entire anterior portion of the parasphenoid tapers to contact the ventral rostral bones (e.g., Grande & Bemis, 1991, figs. 6, 32, 52, 67). However, in our specimens, we found the condition in *Huso* to be more like that of other sturgeons than did Findeis (1993). Kittary (1850, pl. 6, fig. 10) also illustrated a specimen that has a well-developed median process that is distinct from the lateral edges of the parasphenoid.

The anterior tip of the median anterior process of the parasphenoid contacts the posteriormost ventral rostral bone (**vrb**, Figs. 38, 39, 42–46), which were first found developed at 50.4 mm TL. The ventral rostral bones form a series of bones on either side of the ventral midline of the snout and are variable in number and distribution. The anterior ventral rostral bones are typically small, flat, irregularly shaped elements. The posteriormost ventral rostral bone (vb1 of Findeis, 1997) in *A. brevirostrum*, as in other sturgeons, is the longest of the series. The dorsal surface of this element varies from flat or only slightly concave to strongly concave with pointed processes of bone deeply embedded in the cartilage of the chondrocranium. No matter its form, however, it is closely

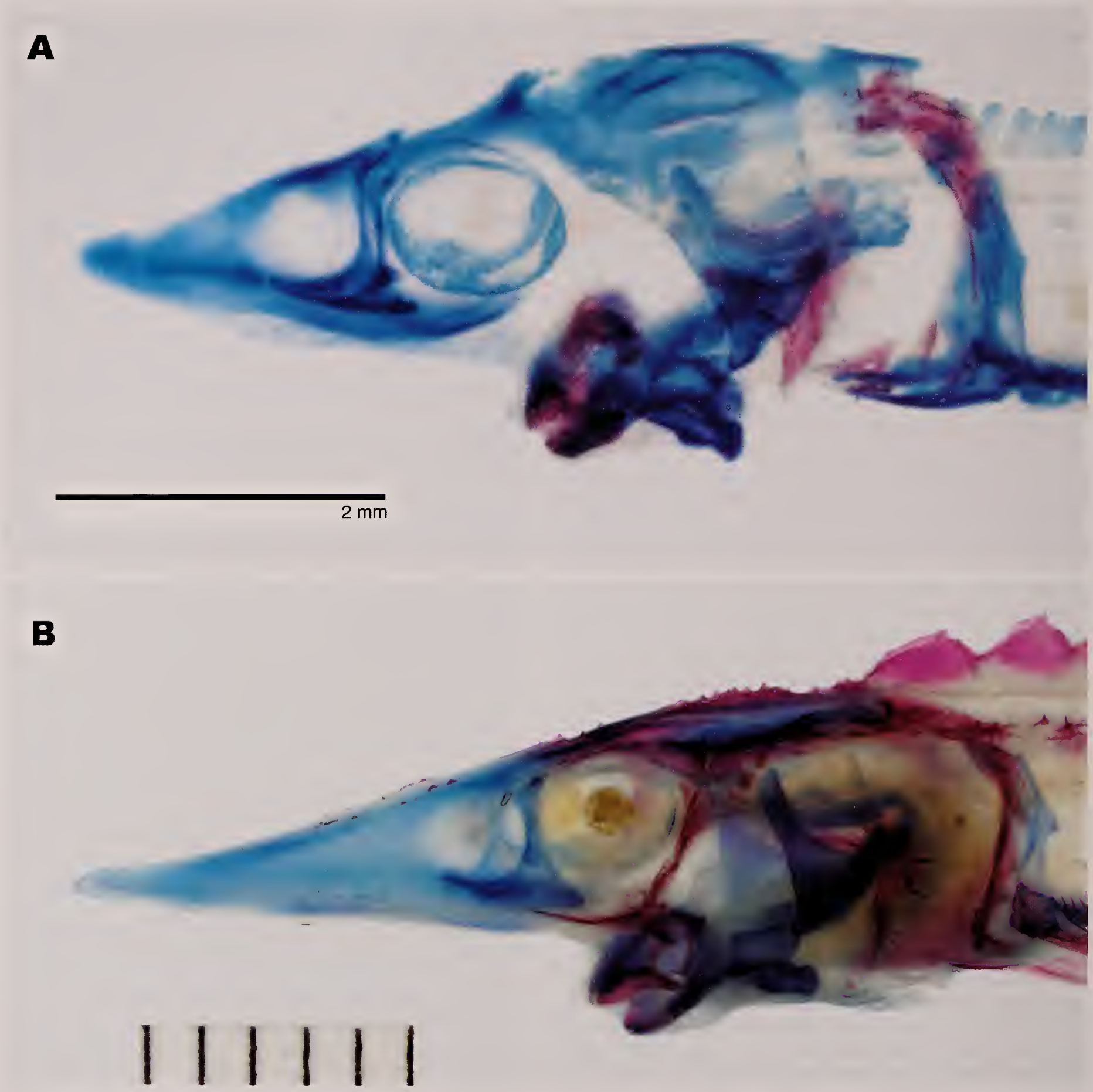
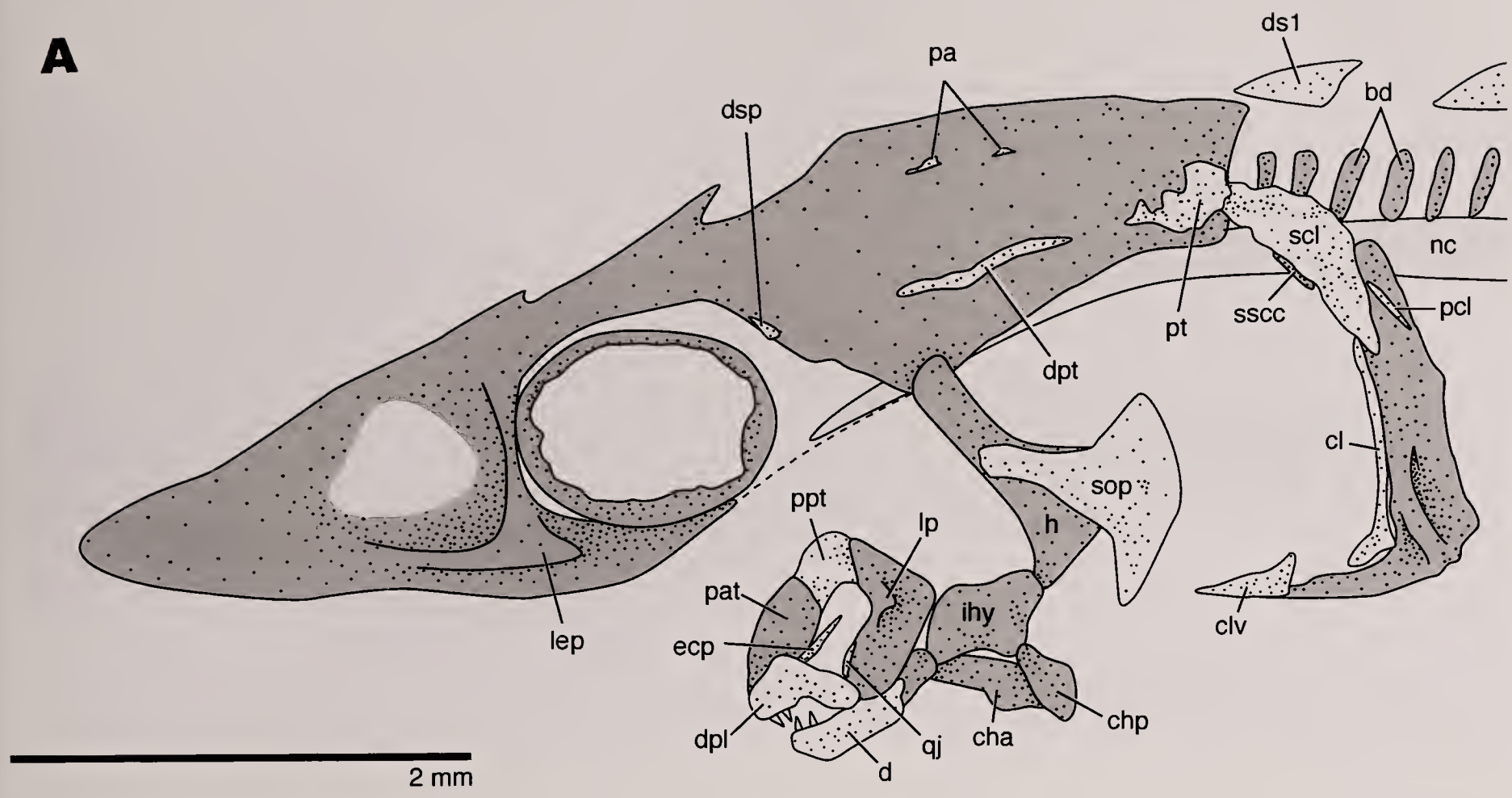


FIG. 35. *Acipenser brevirostrum*, skull and pectoral girdle at early stages of development in lateral view. Note that the dorsal scutes in **A** are very lightly mineralized and do not appear in photo. (**A**) VIMS 12077 (21.9 mm TL). (**B**) VIMS 12082 (58.5 mm TL). Anterior to left. Scale in millimeters.



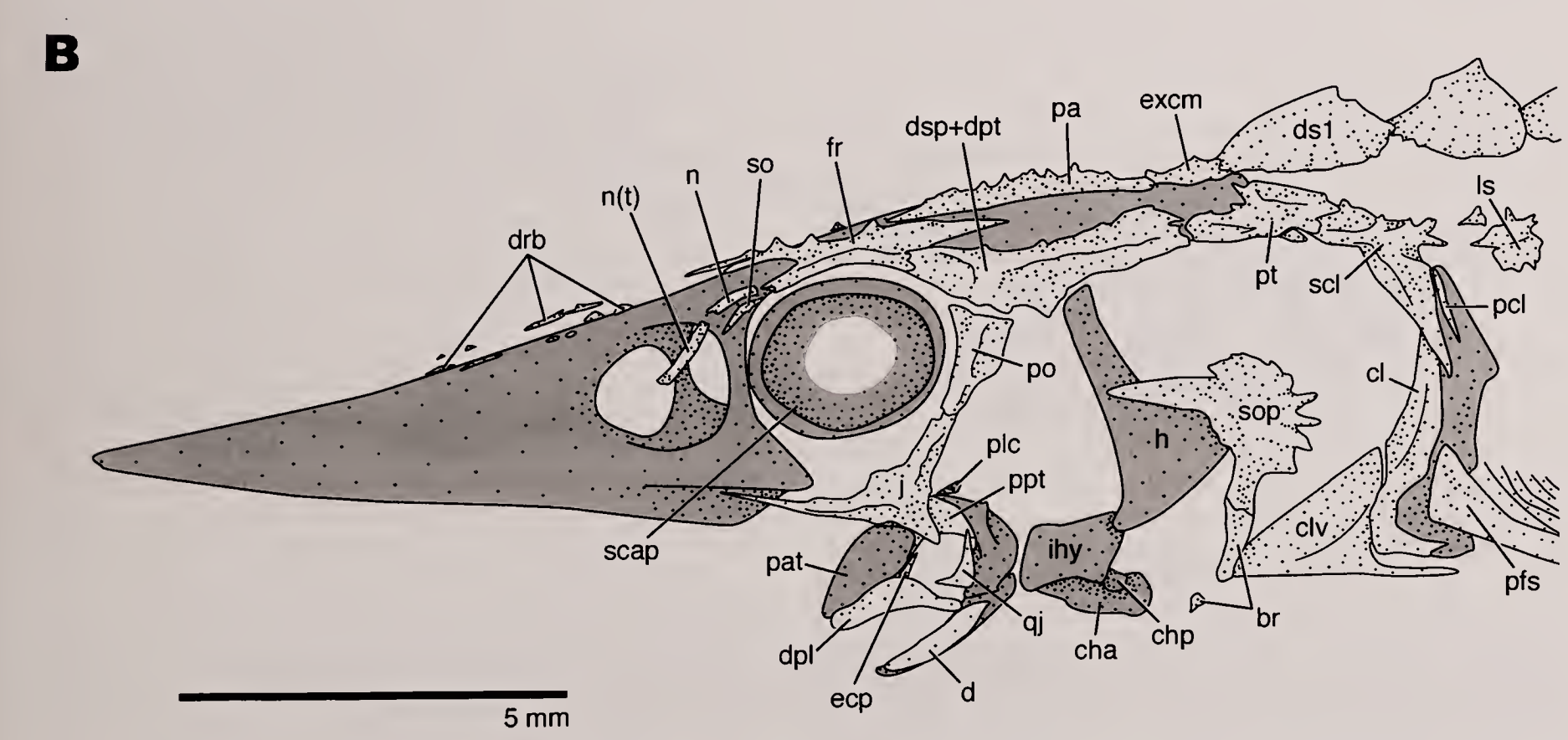


FIG. 36. *Acipenser brevirostrum*, skull and pectoral girdle at early stages of development in lateral view. Line drawing of Figure 35. Abbreviations found on pages 8–9.

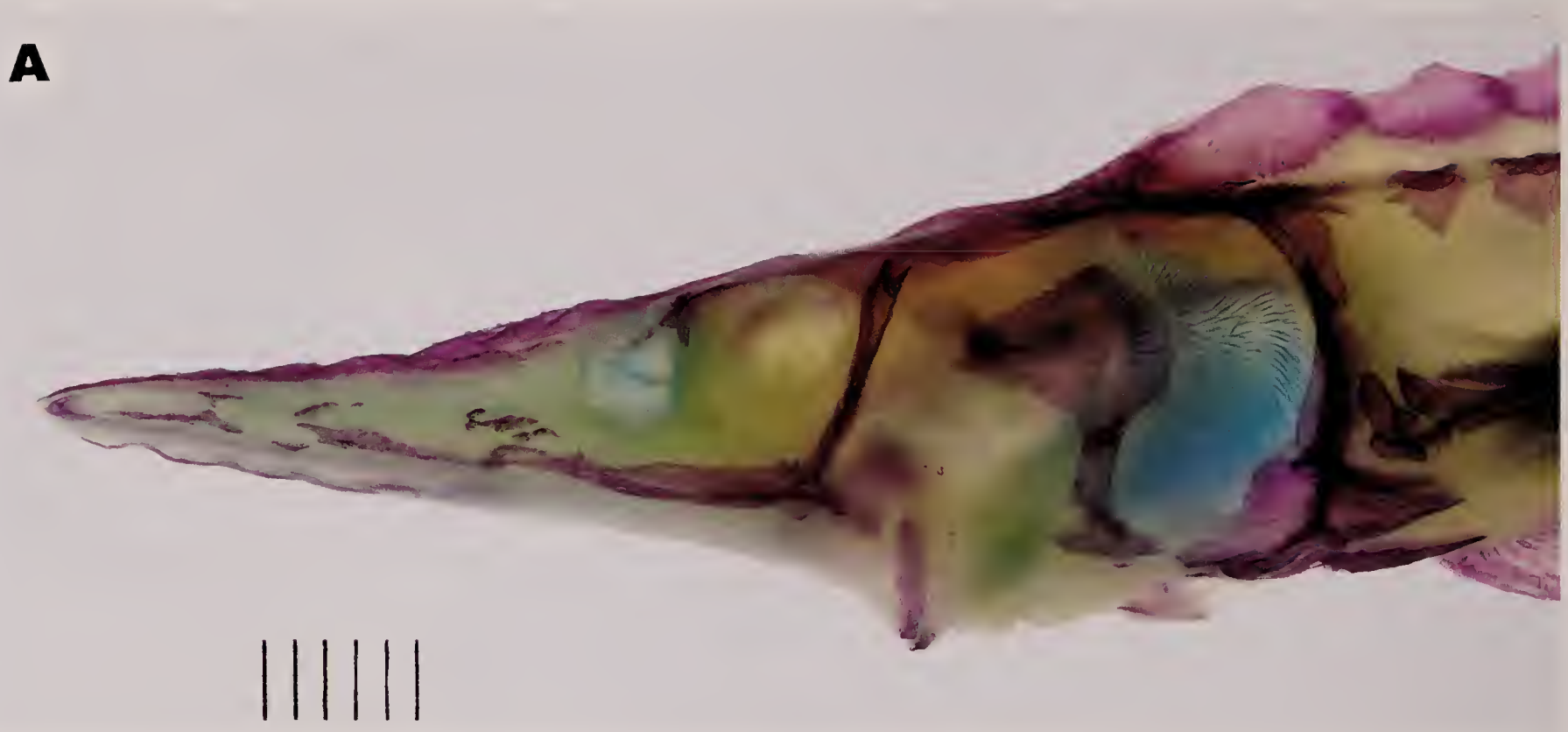


FIG. 37. *Acipenser brevirostrum*, skull and pectoral girdle of small juvenile showing early development of border rostral bones in dorsal view, from VIMS 12084 (127 mm SL). (**A**) Photograph and (**B**) line drawing. Scale in millimeters. Anterior to left. Abbreviations found on pages 8–9.

associated with the ventral surface of the chondrocranium and follows the pronounced ridge along its midline. According to Findeis (1997, fig. 19, character 30), the posteriormost ventral rostral bone is invariably a single median element in most sturgeons, and this is one of the characters in his analysis that supports a basal position of *Huso*, which he found to have a pair of posterior ventral rostral bones, as is found also in polyodontids. Hilton (2005), however, reported one specimen of *Huso* with a single posterior ventral rostral bone, suggesting that this character may be polymorphic—or at least variable—for species in this genus. We also found a single posterior ventral rostral bone in a specimen of *H. huso* that was CT scanned (MCZ 54269). There is a series of ventral rostral bones in polyodontids as well (Grande & Bemis, 1991; Grande et al., 2002); Grande and Bemis (1991) suggested the homology of the posterior pair of ventral rostral bones in polyodontids with the vomers of other actinopterygians.

Sensory Canals, Ampullary Organs, and Sclerotic Capsule

The trunk sensory canal runs the length of the body and pierces each lateral scute in its central part (see the section Scutes). Between scutes, the trunk canal is enclosed in a bony tube. Posteriorly, the trunk canal curves dorsally in smaller, irregularly shaped plates and becomes enclosed by bony tubes. These tubes follow the bases of the caudal fin rays and end near the tip of the tail (Hilton, 2004). Anteriorly, the trunk sensory canal enters the skull to branch into the cephalic sensory canal system. The posttemporal receives the trunk sensory canal from the supracleithrum (**scla**, **sclb**, Fig. 89), and this canal splits, with one branch coursing medially to form the occipital sensory canal (**ocn**, Fig. 19) and the other coursing anteriorly to form the supratemporal sensory canal. The left and right occipital sensory canals meet at a commissure in the median extrascapular bone; this commissure extends far forward in the median extrascapular (Fig. 19).

The supratemporal sensory canal (**stcn**, Fig. 19) passes through portions of the posttemporal, dermopterotic, and dermosphenotic. It is in the dermosphenotic that the supratemporal sensory canal splits to form the supraorbital sensory canal (**socn**, Fig. 19) and the infraorbital sensory canal (**iocn**, Fig. 19). The supraorbital sensory canal arches medially to pass though the frontal bone before entering the nasal bone and terminating at the tubular nasals (Fig. 19), which are positioned between the anterior and posterior nares; the supraorbital canal does not connect with the infraorbital canal anterior to the orbit. Jollie (1969, p. 68) concluded that "originally [i.e., plesiomorphic for Acinopterygii] this canal passed between them [the anterior and posterior nares], whether or not it connected with the infraorbital canal." The infraorbital sensory canal exits the dermosphenotic laterally to pass through the postorbital and jugal before becoming the rostral sensory canal (**rcn**, Fig. 19; see also Hilton, 2002a). The rostral canal is housed in a series of rostral canal bones and loops lateral to the chemosensory barbels (see Findeis, 1997; Hilton, 2002a) before paralleling the midline of the snout. The left and right rostral canals meet at the tip of the snout forming the rostral commissure (see further description and discussion of these bones in the section Braincase).

The only sensory canal of the head that is not directly associated with the bones of the skull roof in *A. brevirostrum* and other sturgeons is the canal homologized with the preopercular sensory canal of other fishes. A few tubular bony elements associated with this canal form a chain of irregularly shaped bones about midway between the jugal and the subopercle (Fig. 22).

The cartilaginous sclerotic capsule (**scap**, Fig. 15, 16, 35, 36) becomes extremely hard in adult specimens and forms a cup supporting the eyeball. It has been reported to support ossifications (e.g., Edinger, 1929; de Beer, 1937; Walls, 1942; Patterson, 1977), most often called "sclerotic" bones, although the presence of these bones is variable and their precise identification has been debated. They are easily lost or overlooked, and some reported absences may be due to loss during specimen preparation. These elements do not appear to have a direct connection to the cartilaginous sclerotic capsule but rather are positioned adjacent to the cartilage in the connective tissue (T. Franz-Odendall, pers. comm.). This suggests a different developmental pattern than found in teleosts, in which they are perichondral or endochondral bone forming in the sclerotic cartilage (Franz-Odendall and Hall, 2006; the precise tissue association of the sclerotic bones in other nonteleostean actinopterygians is unknown). Edinger (1929, fig. 8b) illustrated a histological section showing the sclerotic bone of sturgeons within the conjunctiva and overlapping the margin of the sclerotic capsule (see also the description of the sturgeon eye, based on *A. fulvescens*, by Walls, 1942). The smallest specimen in which we found these ossifications was a 472 mm SL cleared and stained specimen (MCZ 54167). The bones are slender and positioned dorsally and ventrally (see Fig. 22). Among Acipenseriformes, "sclerotic" bones have also been found in †*Chondrosteus* (Watson, 1925, fig. 8; Hilton & Forey, 2009, fig. 10) and †*Protopsephurus* (Grande et al., 2002, figs. 8, 10, in which they are greatly reduced), but they are more widespread among basal actinopterygians, some of which have four or more ossicles (Lund, 2000; Franz-Odendall & Hall, 2006).

There are eight distinct pairs of fields or clusters of ampullary organs on the heads of sturgeons (Figs. 20, 21; see Northcutt, 1986). The extent of each of these fields is inter- and intraspecifically variable (e.g., the dorsal rostral series are more extensive in *Scaphirhynchus* than in *A. brevirostrum*; ef. Fig. 21 and Findeis, 1993, fig. 21B), although all are generally recognizable; some of these may blend together and there may be ampullary organs outside these distinct fields as well. Within each field, the ampullary organs are arranged in groups, or rosettes (Findeis, 1993), although the number of organs in each rosette is variable. By far, the largest and most extensive field is the ventral rostral ampullary field, which covers the entire ventral surface of the rostrum except for a narrow strip of skin covering the ventral rostral bone along the midline of the snout. The dorsal rostral ampullary field is restricted to the lateral edge of the dorsal surface of the snout and is situated above the fenestrae among the border rostral bones. Posterior to the dorsal rostral ampullary field is the suborbital ampullary field, which is associated with the posteriormost border rostral bones, the jugal, and the skin immediately dorsal to these bones. On the dorsal surface of the postrostral portion of the skull roof, there are three pairs of ampullary fields: the supraorbital, middle, and occipital fields (anterior to posterior, respectively). The largest of these are the supraorbital ampullary fields, which may be supported by the nasals, supraorbitals, frontals, and the dermosphenotics. The middle ampullary fields are found on the dermopterotic and frontals. The occipital ampullary fields are arranged transversely on the posttemporals, the median extrascapular,

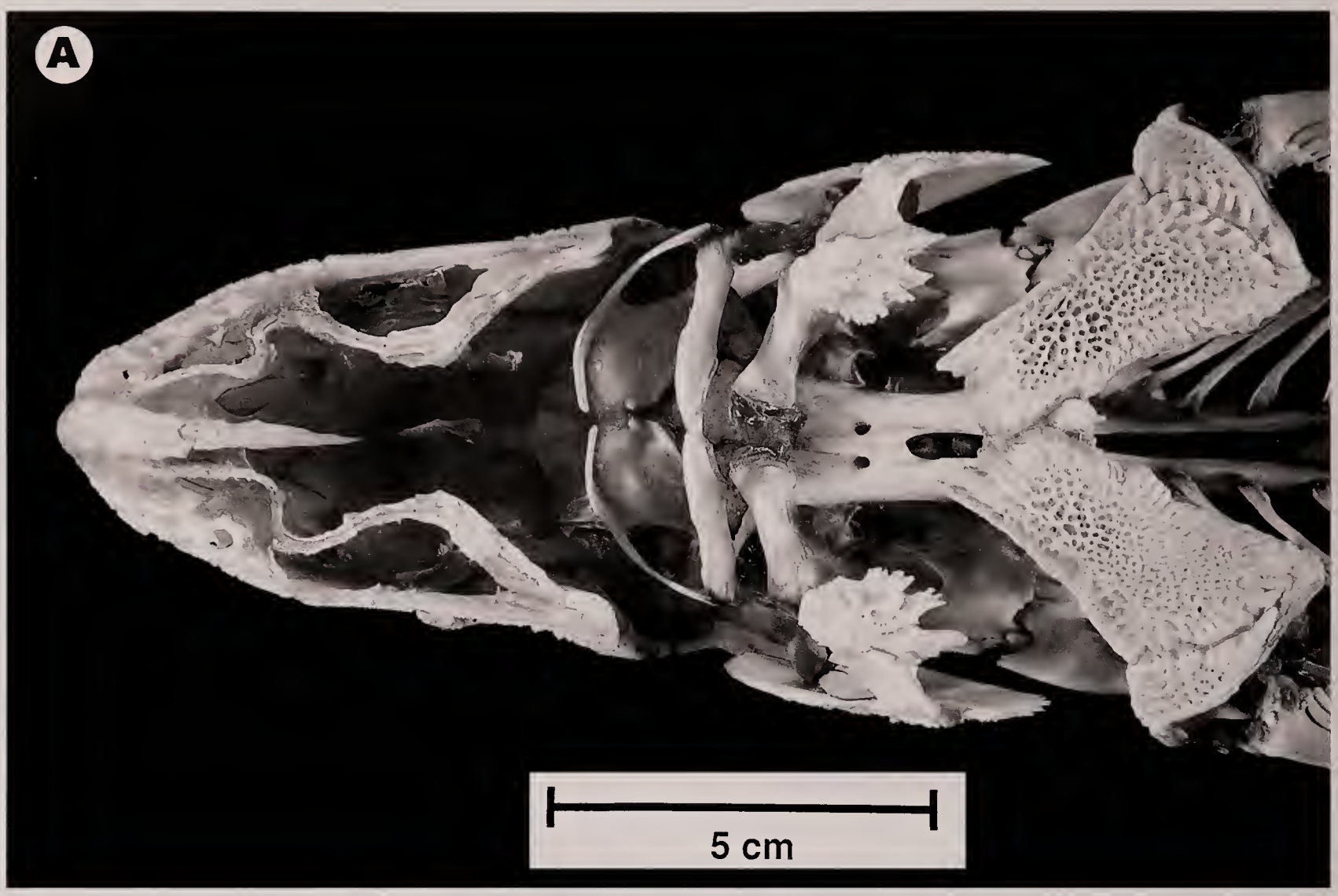


FIG. 38. *Acipenser brevirostrum*, skull and pectoral girdle of adult in ventral view, from FMNH 112212 (sex unknown, 710 mm SL). (**A**) Photograph and (**B**) line drawing. Slight distortion of specimen due to displacement of elements during drying. Branchial arches removed from specimen. Note the unusual presence of border rostral bones (**brb**) on the ventral surface of snout. Most soft tissue and cartilage present on this specimen have been omitted from the line drawing. Anterior to left. Abbreviations found on pages 8–9.

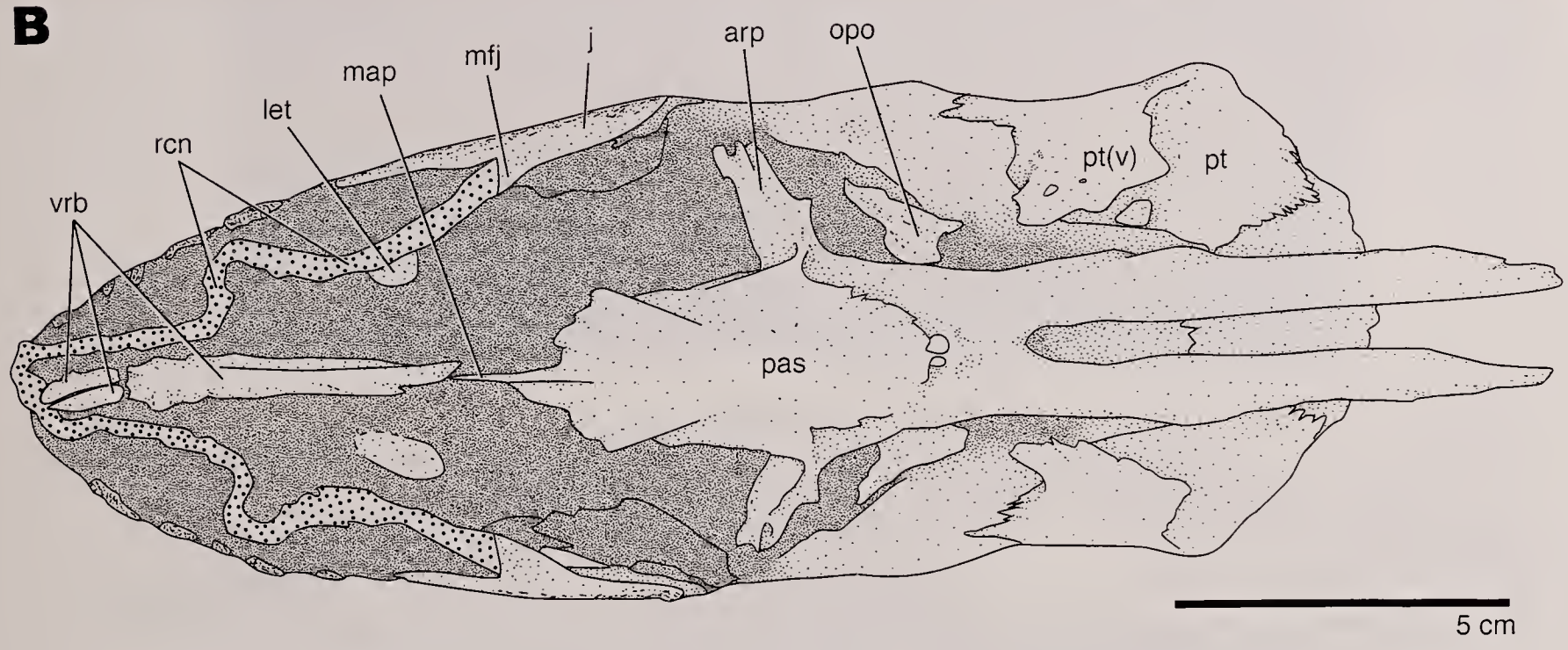


FIG. 39. *Acipenser brevirostrum*, dermal bones of the skull roof and portions of the neurocranium in ventral view, from UMA F10431 (male, 930 mm SL). (**A**) Photograph and (**B**) line drawing. Rostral canal bones in this specimen are covered by connective tissue; they and the course of the rostral sensory canal are indicated in gray with large stipple (see Figs. 43 and 44 for details of rostral canal bones). Most soft tissue and all cartilage present on this specimen have been omitted from the line drawing. Note that the ventral rostral bones are slightly displaced because of drying of the associated cartilages. Anterior to left. Abbreviations found on pages 8–9.

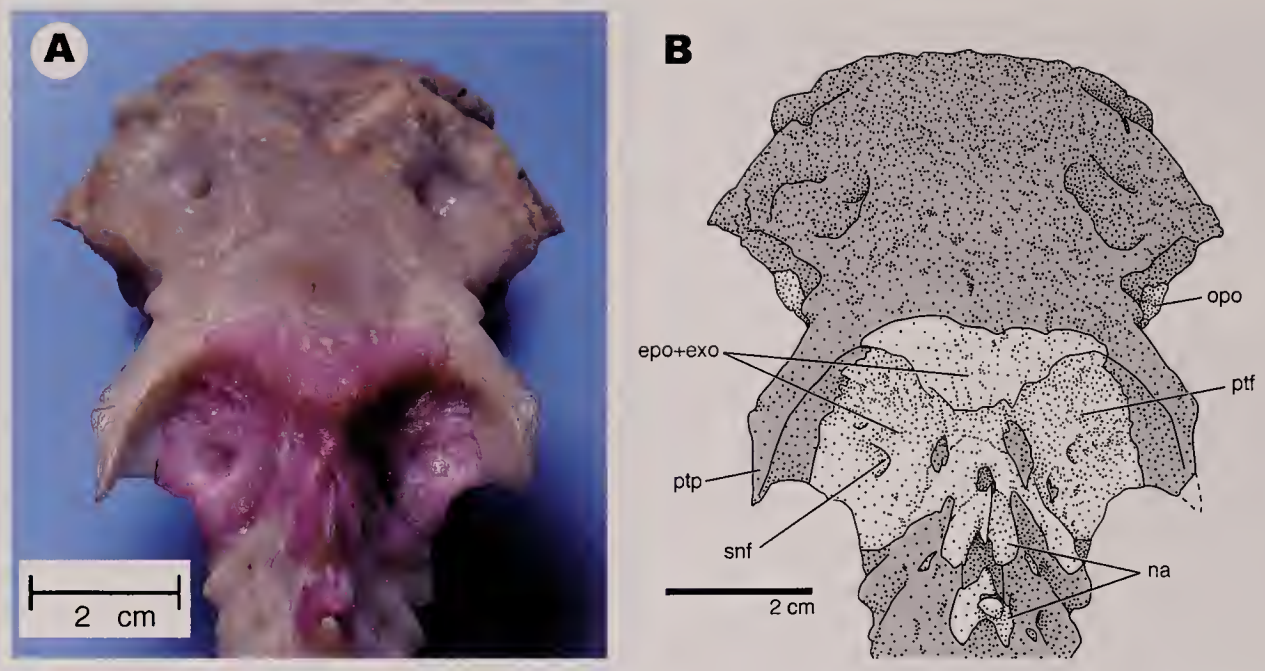


FIG. 40. *Acipenser brevirostrum*, neurocranium in posterior (slightly dorsal) view, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing. In photo, bone is stained red, and cartilage appears white; in drawing, bone is white, and cartilage is gray. Abbreviations found on pages 8–9.

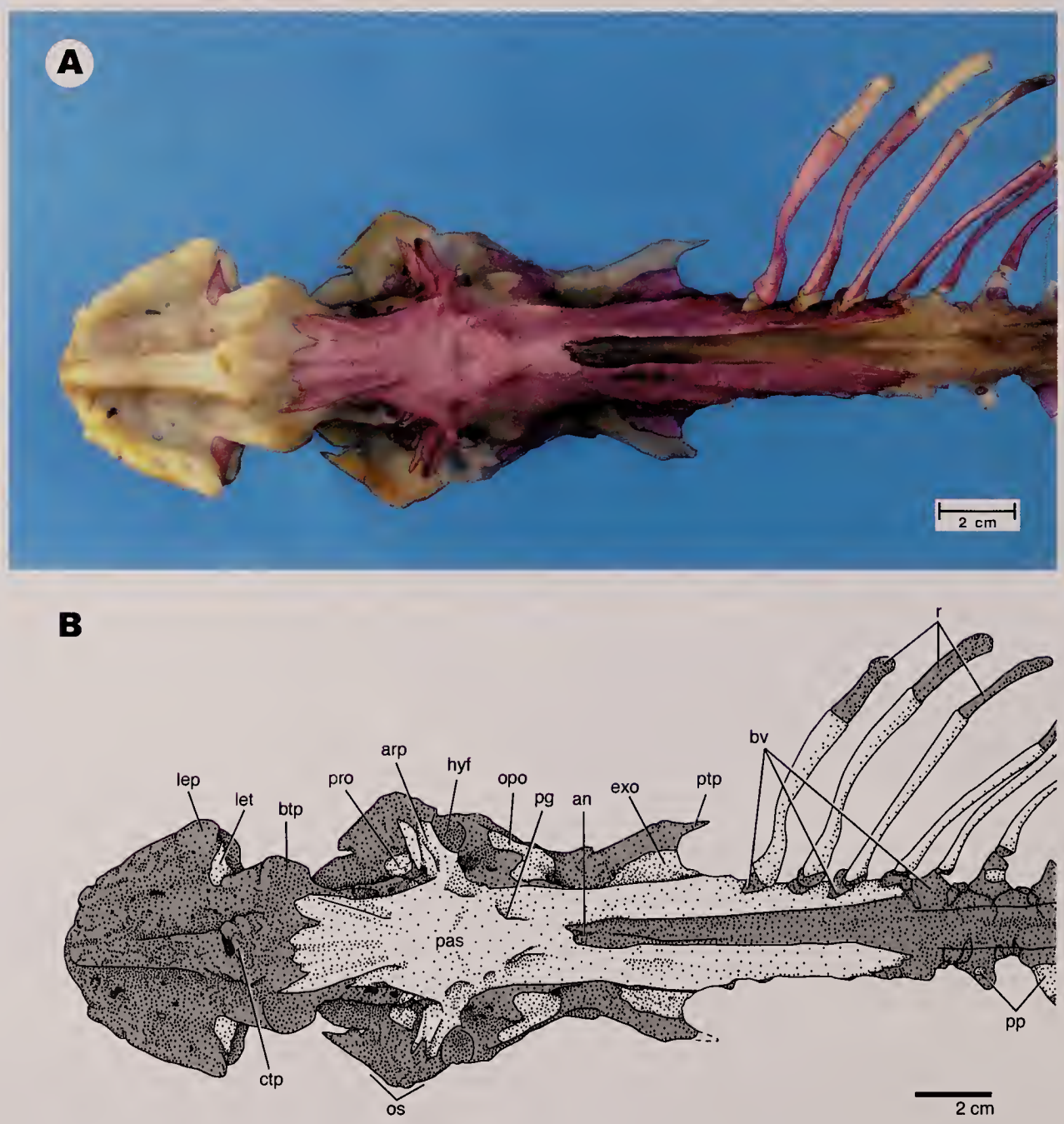


FIG. 41. *Acipenser brevirostrum*, neurocranium in ventral view, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing. In photo, bone is stained red, and cartilage appears white; in drawing, bone is white, and cartilage is gray. Abbreviations found on pages 8–9.

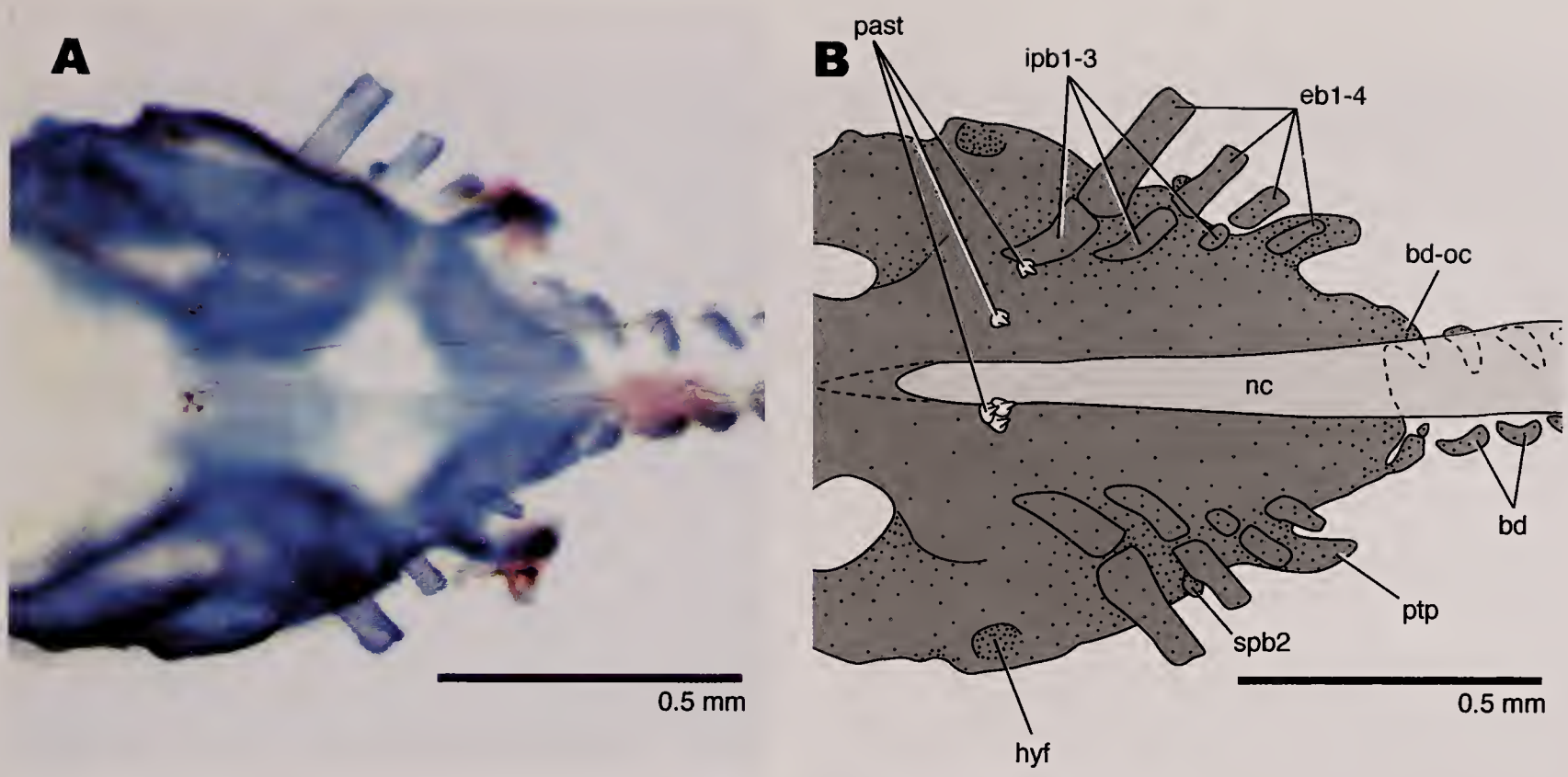


FIG. 42. *Acipenser brevirostrum*, ventral view of braincase in small individuals. (**A**) Photograph and (**B**) line drawing showing parasphenoid tooth patches, from VIMS 12076 (22.1 mm TL). (**C**) Photograph and (**D**) line drawing of a juvenile with mouthparts, ventral portion of gill arches, and pectoral girdle dissected away to show articulation of dorsal gill arches with braincase and general anatomy of the ventral neurocranium and associated skeletal structures, from VIMS 12086 (71 mm SL). Abbreviations found on pages 8–9.

and possibly the parietals (the posteriormost tip of the parietal may support some of the rosettes). On each side of the lateral surface of the head behind the eye are two series of ampullary organs—the preopercular ampullary field, immediately posterior to the eye, and the opercular ampullary field, which is associated with the subopercle and branchiostegals. Both of these series curve ventrally onto the ventral surface of the head. All ampullary fields found closely associated with dermal bones may, to a varying degree, interrupt the ornamentation, ranging from nearly indistinguishable to relatively broad spaces of smooth, unornamented underlying dermal bone.

Opercular Series

The opercular series in *A. brevirostrum* and that of Acipenseridae generally consists of a large plate-like subopercle and typically two branchiostegals; the preopercle, opercle, and interopercle are absent. Grande et al. (2002) considered that loss of the opercle was convergent in Acipenseridae and all Polyodontidae except for †*Protopsephurus*.

The subopercle (**sop**, Figs. 8, 16, 18, 26, 35–38, 47–51) is a large, ornamented plate of bone, with a more or less distinct anterior extension, although the overall shape of the subopercle is subject to great variation (Figs. 50, 51). This anterior extension in *A. brevirostrum*, as in other species of *Acipenser*, is not as narrow and distinct as that found in †*Priscosturion*, *Scaphirhynchus*, and *Pseudoscaphirhynchus* (e.g., Tatarko, 1936, pl. 4, fig. 12; Grande & Hilton, 2006, fig. 20). The anterodorsal and posterior margins of the subopercle are scalloped. The anterior portion of the lateral surface of the subopercle is largely unornamented and is covered by a thick layer of skin. Perhaps correlated with reorganization of the mouthparts of acipenserids and loss of most elements of the opercular series, there is no discrete joint between the subopercle (which effectively has taken the place of the opercle as the largest bone supporting the opercular region) and the hyomandibula. Instead, the cartilaginous portion of the hyomandibula, which is broad distally, is closely associated with the inner surface of the subopercle. The subopercle is among the first bones of the skull to ossify and is present in an 18.8 mm TL specimen as a thin splint of bone lateral to the hyomandibula. This splint establishes the long axis of the anterior extension of the subopercle.

The ventral portion of the subopercle forms a broad overlapping suture with the dorsal branchiostegal (**br**, Figs. 26, 38, 47–51). There typically are two branchiostegals present in *A. brevirostrum*, although there is substantial variation in the number, shape, and arrangement of the ventral branchiostegals (Figs. 50, 51; Table 3). The dorsalmost branchiostegal is invariably a relatively tall element and is the first to ossify (by 21.9 mm TL). In the adult, there is a distinct concavity on the lateral surface of this branchiostegal, and it is typically unornamented or at least bears little ornament on its superficial surface. The ventral branchiostegal is typically heavily ornamented, flat, and broad anteroposteriorly, although it is irregular in shape and has a roughly serrated posterior margin. There may be additional smaller ventral branchiostegals, although one element always is the largest. The ventral branchiostegal was first found to be present as a tiny ossification in a 42.3 mm TL specimen.

Palatoquadrate and Its Ossifications

The palatoquadrate and associated bones of acipenserids have been illustrated or described by Parker (1873, 1882), de Beer (1925), Sewertzoff (1926c, 1928), Bugajew (1930), Tatarko (1936), Stengel (1962), Jollie (1980), Arratia and Schultze (1991), Findeis (1993), Bemis et al. (1997), and Tsessarskii (2001), among others; portions of the palatoquadrate and the lower jaw joint for several acipenserids were also illustrated by Antoniu Murgoci (1936a,d, 1942).

The upper jaws of sturgeons are significantly derived relative to the "typical" basal actinopterygian condition (e.g., †*Cheirolepis*; Arratia & Cloutier, 1996) due to the radical restructuring of the jaw apparatus associated with the ventral orientation of the jaws and their "shark-like" protrusibility. All acipenserids lack ossifications that correspond to those of the upper jaws of other actinopterygians (i.e., maxillae and premaxillae; Bemis et al., 1997). The absence of these bones is considered a synapomorphy of Acipenseriformes by Bemis et al. (1997, character 11; see also Grande & Bemis, 1996, Grande et al., 2002; Grande & Hilton, 2006). The element that we refer to as the dermopalatine was historically interpreted as the maxilla. Sewertzoff (1926c, 1928; see also Stengel, 1962, fig. 1) considered this element to be a fused premaxilla and maxilla, citing developmental evidence of two distinct tooth patches (i.e., one corresponding to that of the premaxilla and one to that of the maxilla) in larval specimens of *Acipenser*. While this bone does form as two distinct elements (Findeis, 1991), it is more parsimonious, as pointed out by Grande et al. (2002, p. 225), to "interpret this condition as resulting from only one change (loss of the maxilla), with the dermopalatines being retained in their plesiomorphic position as ensheathing elements of the palatoquadrate cartilage" than to interpret the maxilla to have been incorporated into the palatoquadrate arch.

The ventral surface of the roof of the mouth (i.e., the palatoquadrate) of adult specimens of *A. brevirostrum*, as in all other Acipenseridae, is edentulous. In larval and small juvenile stages, however, there are two paired tooth rows: one associated with the dermopalatine and one with the palatopterygoid (Fig. 58). In larvae, the dermopalatine bears a single row of teeth that oppose those of the dentary. The dermopalatine teeth are lost by 27.6 mm TL; traces of the tooth sockets are still apparent following this stage, although the bone soon becomes smooth. There are also elongate patches of teeth, arranged in two irregular rows, which form more posteriorly and are associated with the palatopterygoid bone; these tooth patches persist until about 42 mm TL.

In all acipenserids, the dermopalatine (**dpl**, Figs. 26, 35, 36, 38, 52–58) is the anteriormost bone of the palatoquadrate and defines its entire anterior margin. It was beginning to ossify in our 18.8 mm TL specimen. Medially, the dermopalatine contacts the palatine region of the palatoquadrate cartilage (the autopalatine bone comes close to contacting the dermopalatine but is separated from it by cartilage, even in large specimens; Fig. 52). In dorsal view, the medial half of the dermopalatine of *A. brevirostrum* is broader than the lateral half. There is a smooth curve to the dermopalatine of *A. brevirostrum* in dorsal view (Fig. 52; a similar condition is found in *A. fulvescens*; Grande & Bemis, 1991, fig. 79), in contrast to the sharp bend found in *A. oxyrinchus* (e.g., USNM 110207), *A. sturio* (e.g., AMNH 215830SD), and other

FIG. 43. *Acipenser brevirostrum*, disarticulated dermal bones from the ventral surface of the neurocranium mostly in dorsal view (postorbital and jugal in lateral view), from UMA F10547 (male, 915 mm SL). (**A**) Photograph and (**B**) line drawing. Anterior to left. Abbreviations found on pages 8–9.

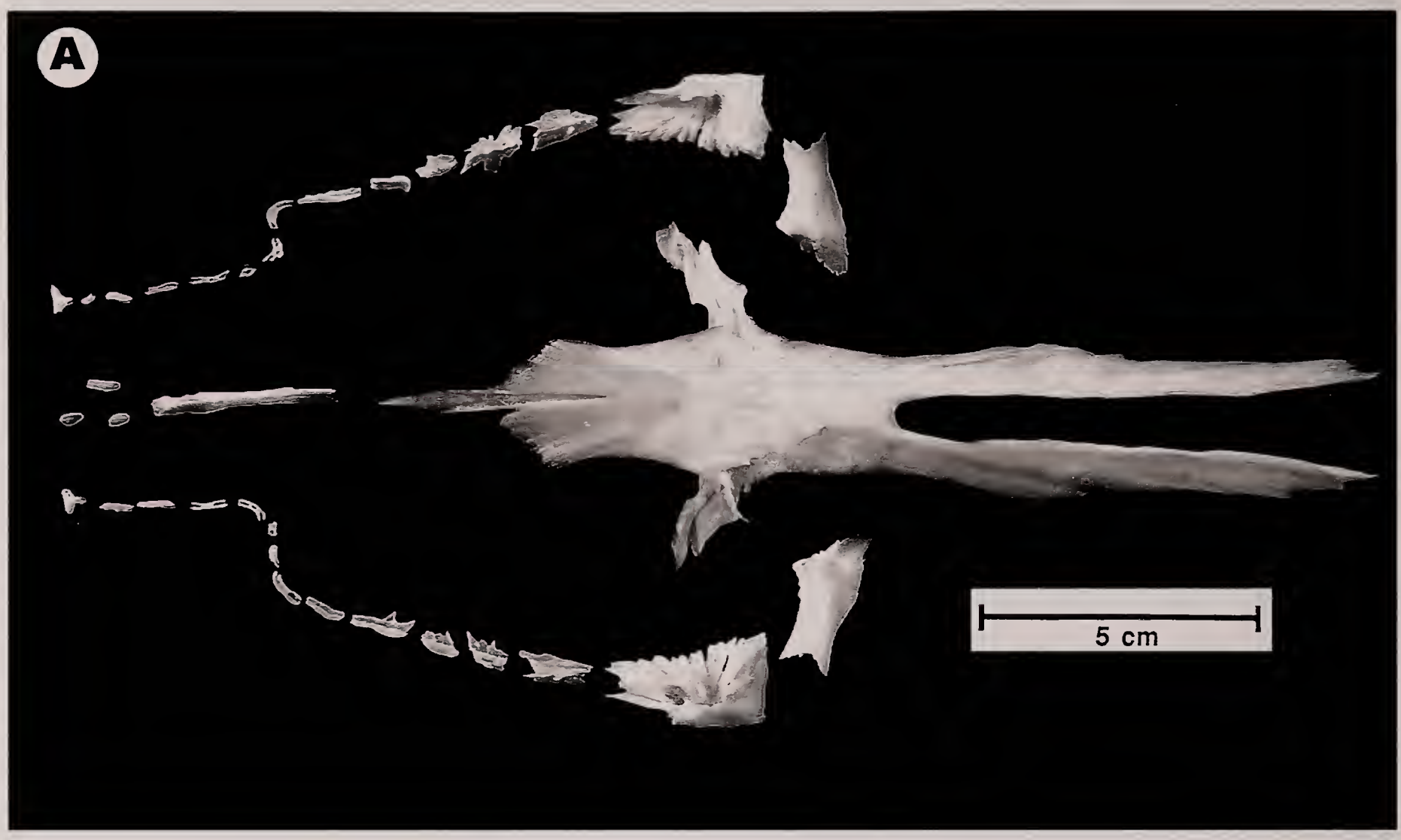


FIG. 44. *Acipenser brevirostrum*, disarticulated dermal bones from the ventral surface of the neurocranium mostly in ventral view (postorbital and jugal in medial view), from UMA F10547 (male, 915 mm SL). (**A**) Photograph and (**B**) line drawing. Anterior to left. Abbreviations found on pages 8–9.

species of *Acipenser* (see Fig. 133). Laterally, the dermopalatine contacts the quadratojugal, when developed, along its dorsolateral edge.

Three bones—the ectopterygoid, quadratojugal, and quadrate—form a bridge between the dermopalatine and the lateral portion of the palatoquadrate in *A. brevirostrum*. The ectopterygoid (**ecp**, Figs. 26, 35, 36, 38, 52–56) broadly contacts the dermopalatine, but the two were always found to be separate, even in the largest specimens examined. The ectopterygoid is a relatively slender bone that forms a bridge between the dermopalatine and the broad anterior flange of the palatopterygoid to form the medial portion of a fossa for the adductor mandibulae. The quadratojugal (**qj**, Figs. 26, 35, 36, 52–58) is a slight, J-shaped bone that contacts the dermopalatine anteriorly and the quadrate and palatopterygoid posterolaterally. Arratia and Schultze (1991) considered the presence of a quadratojugal not associated with a vertical pit line to be characteristic of Acipenseriformes. Both the ectopterygoid and the quadratojugal were found in 21.0 mm TL specimens. The perichondral quadrate (**q**, Figs. 52, 56, 57) bridges the space between the quadratojugal laterally and the palatopterygoid medially. Together with its associated cartilage, the quadrate forms the dorsal portion of the lower jaw joint.

The palatopterygoid (**ppt**, Figs. 26, 35, 36, 38, 52–58) is the largest bone of the palatoquadrate and has three distinct regions. Anteriorly, a broad process contacts the ectopterygoid ventrally and the autopalatine dorsally and forms the dorsomedial portion of the fossa for the adductor mandibulae. This fossa is formed also by the ventrolateral process of the palatopterygoid, which contacts the cartilage associated with the quadrate. The medial process of the palatopterygoid broadly contacts the autopalatine in adult specimens (Figs. 53, 55, 56). The medial processes of the left and right palatopterygoid of *A. brevirostrum* approach each other in the midline (visible in ventral view; Fig. 53). In *A. oxyrinchus* (e.g., USNM 110207) and *A. sturio* (e.g., AMNH 215830), the medial processes are narrower and more elongate and broadly contact each other in the midline. The ventral surface of the palatopterygoid of *A. brevirostrum* is marked by a strong ridge of bone along its posterior axis. The palatopterygoid initially develops as a bony outgrowth from a patch of teeth (the teeth were present in an 18.8 mm TL specimen, but the actual bone of the palatopterygoid was not observed in specimens smaller than 20.5 mm TL).

The autopalatine (**ap**, Figs. 52–57) is a large circular or squarish perichondral bone that develops in the medial portion of the palatoquadrate cartilage (i.e., the *pars autopalatina*). In large adults, the autopalatine contributes to the symphysis between the left and right palatoquadrates and is pierced by a foramen for the *nervus labialis* (Stengel, 1962); this foramen is entirely in cartilage in small specimens.

Posterior to the bones and cartilages of the palatoquadrate is a complex of thick, flat cartilaginous sheets that cross the midline of the roof of the mouth (**plc**, Figs. 36, 52, 53, 58). These cartilages have been referred to by several names, including the metapterygoid (Parker, 1873, 1882), the lateral and medial postpalatine laminae and styles (Bugajew, 1930), the pharyngeal cartilages (Antoniu Murgoci, 1936d), the postpalatine cartilages (Antoniu-Murgoci, 1942), the cartilago impar (Edgeworth, 1935), the mouth-roof cartilages (de Beer, 1937; Arratia and Schultze, 1991), and the palatal complex (Findeis, 1993, 1997); we follow Findeis's terminology here. The palatal complex of *A. brevirostrum*, as in all acipenserids, displays significant individual variation, although the overall shape of the complex is similar between specimens (e.g., see Antoniu Murgoci, 1942, figs. 14, 15, for examples from *A. gueldenstaedti* and *A. ruthenus*, respectively). There are never tooth plates associated with the palatal complex, although in several specimens we observed small perichondral ossifications on its ventral (i.e., oral) surface.

Lower Jaw

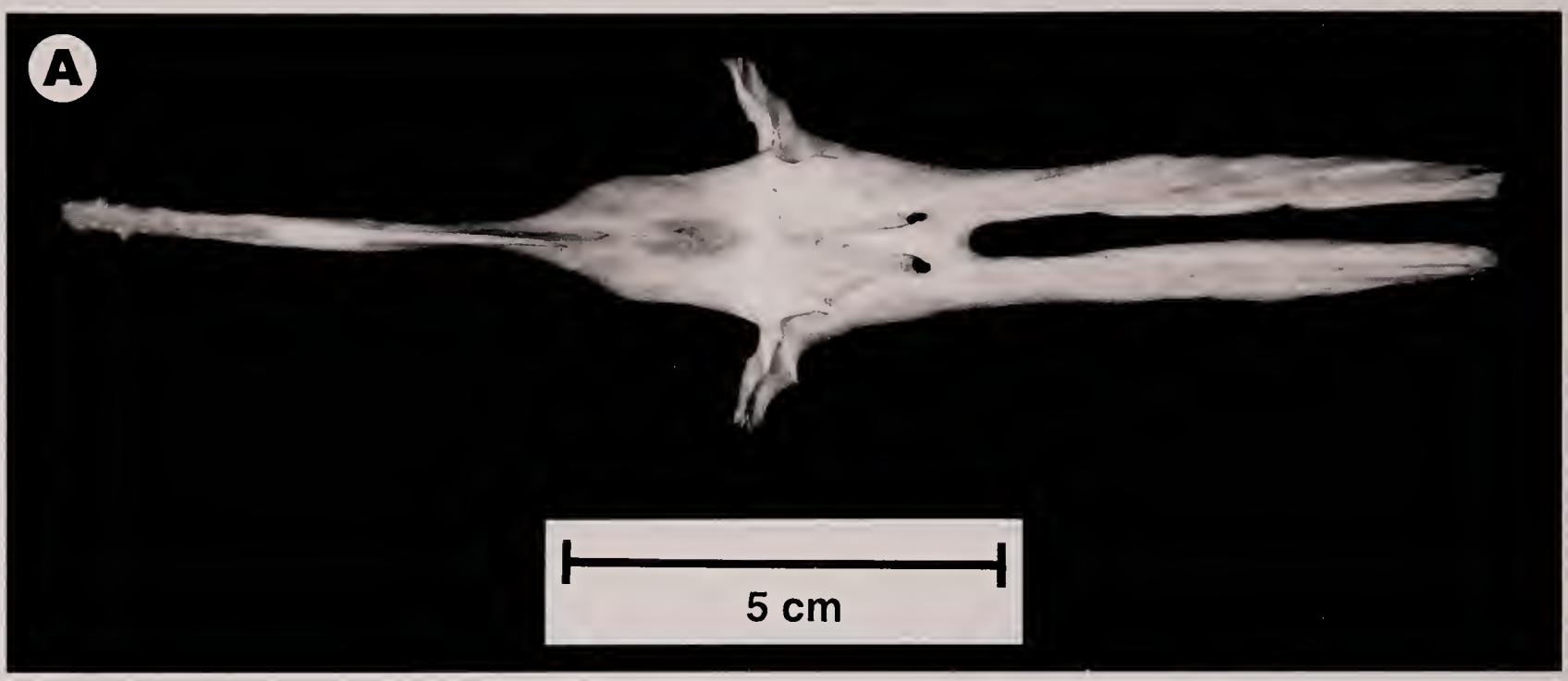
The lower jaw of extant Acipenseridae was described and illustrated by Parker (1873, 1882), Sewertzoff (1926c, 1928), Bugajew (1930), Tatarko (1936), Jollie (1980), Findeis (1993), Bemis et al. (1997), and Tsessarskii (2001), and the jaw joint of several acipenserids was illustrated by Antoniu Murgoci (1936a,d, 1942). The lower jaw of *Acipenser* typically consists of two dermal bones (dentary and prearticular) and a single chondral bone (mentomeckelian) surrounding Meckel's cartilage; as described below, we discovered an ossified articular in a single large specimen examined here. The joint between the lower jaw and quadrate of *A. ruthenus* was illustrated in cross section by Haines (1942, fig. 4), who determined that the joint was of a schizarthrosis type (i.e., there are several small cavities in the joint) but considered this to be a secondary condition derived evolutionarily from an eudiarthroses (i.e., synovial) type of jaw joint, which is found in most jaw joints, including other basal actinopterygians (e.g., *Polypterus*, *Lepisosteus*, and *Amia*).

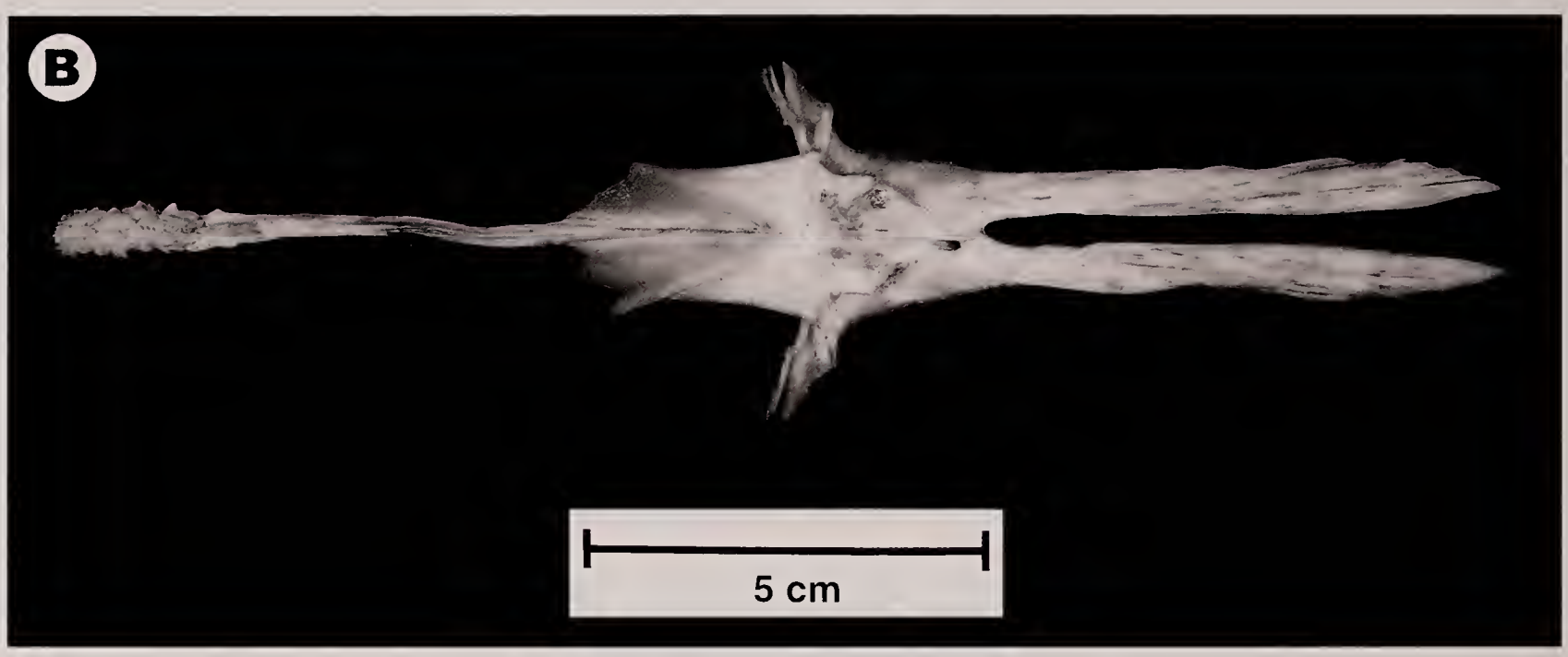
The largest bone of the lower jaw is the dentary (**d**, Figs. 26, 35, 36, 38, 59–63), and it is already well ossified in our smallest specimens. This bone is roughly rectangular in lateral view, although it tapers slightly anteriorly. In dorsal view, it is slightly sigmoidal (Fig. 59). A groove on its anteromedial surface accommodates the mentomeckelian. In larvae, the dentary bears a row of teeth that are opposed by those of the dermopalatine; these teeth are lost by 27.6 mm TL.

A thin splint-like dermal prearticular (**par**, Figs. 59–63) was first observed in specimens of 58.5 mm SL and is positioned along the dorsomedial surface of the dentary. In some specimens, the prearticular has grown posteriorly to approach the articulatory surface of the lower jaw. Because the tendon of *m. adductor mandibulae* attaches directly to the cartilage, Starks (1916) concluded that this bone is the prearticular (= his splenial) and that the coronomeckelian (= his sesamoid articular) is absent in sturgeons; we agree with this interpretation.

A thin but well-developed perichondral mentomeckelian bone (**m**, Figs. 59–62) is present in adult specimens of *A. brevirostrum*. This bone completely surrounds Meckel's cartilage and is positioned on its anterior half and serves as the attachment site of the *m. geniobranchialis*, which also attaches to the third hypobranchial (pers. obs.). This is the only ossification of Meckel's cartilage found in all adults examined in this study. A mentomeckelian in *Acipenser* was also reported by Starks (1916) and Grande and Bemis (1991, fig. 79).

We found a thin, circular perichondral bone the articular region of Meckel's cartilage in one of our largest specimens (UMA F10578, 890 mm SL). This bone is positioned on the surface of the dense portion of Meckel's cartilage, where it articulates with the *pars quadrata*, and we interpret this ossification to be homologous to the articular of other actinopterygians (**ar**, Fig. 61). To our knowledge, this is the first report of an articular in any extant acipenseriform. However, the presence of this bone is variable, as specimens of similar or even





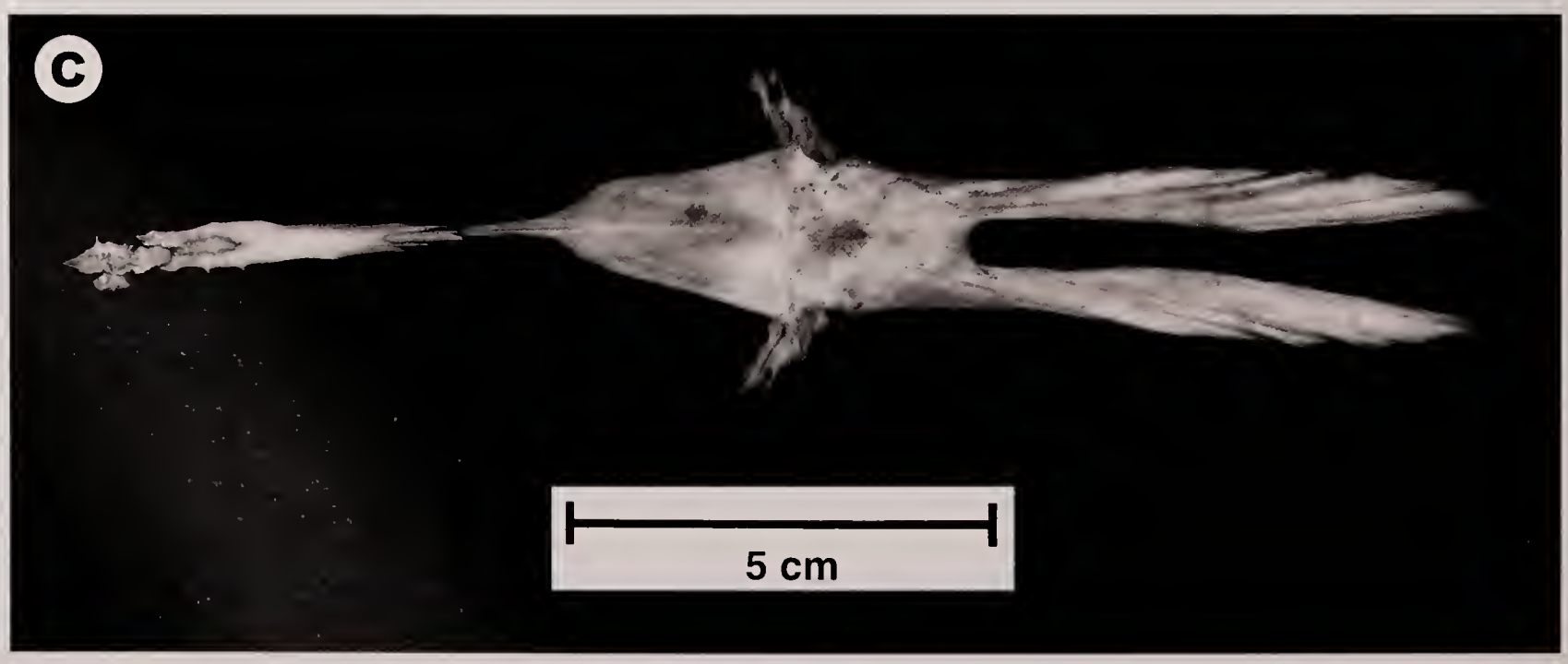


FIG. 45. *Acipenser brevirostrum*, ventral view of parasphenoid and ventral rostral bones showing variation in patterns of ossifications and presence of foraminae for the efferent branchial arteries. (**A**) VIMS 12073 (female, 660 mm SL). (**B**) VIMS 12074 (female, 695 mm SL). (**C**) VIMS 12071 (male, 705 mm SL). Anterior to left.

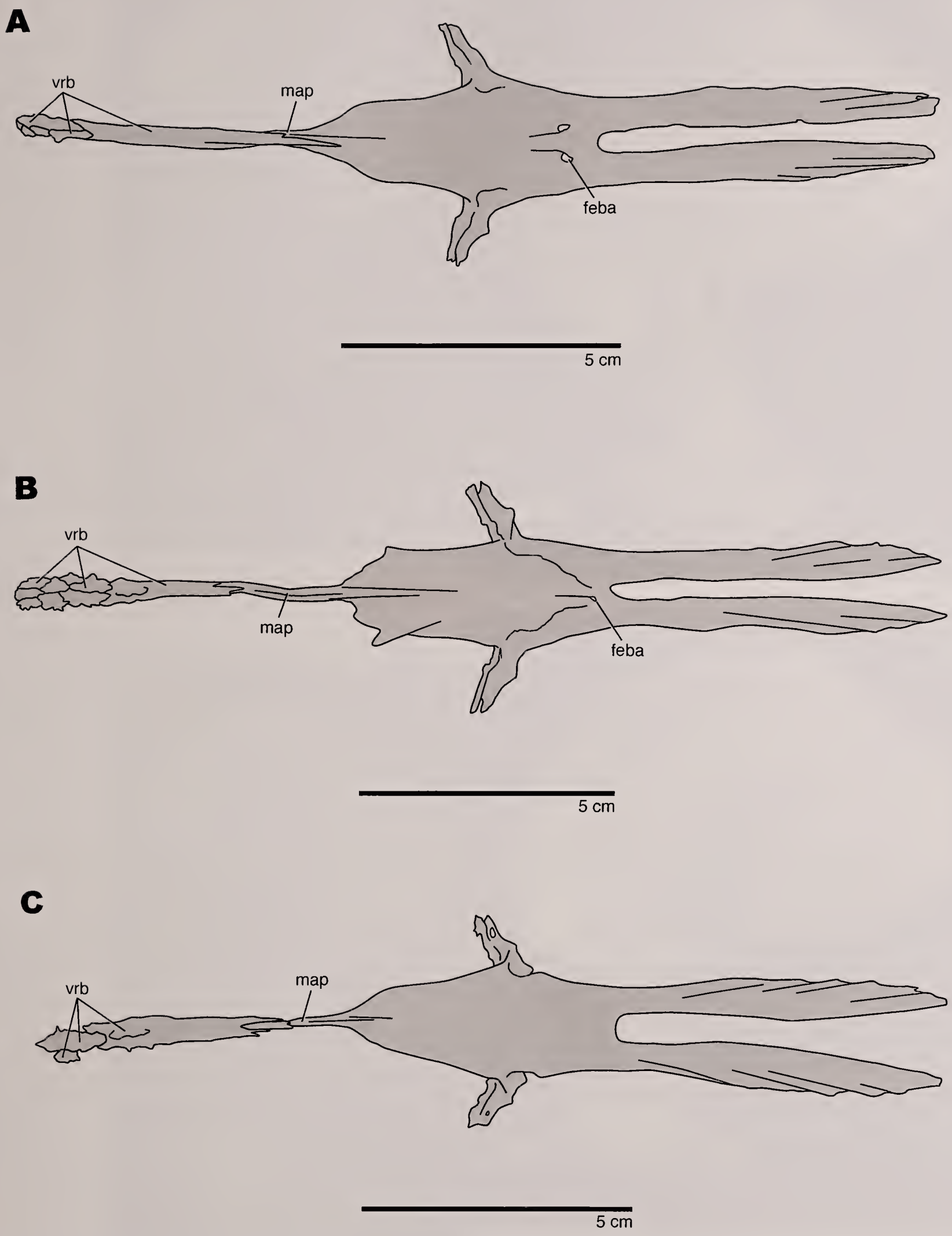


FIG. 46. *Acipenser brevirostrum*, ventral view of parasphenoid and ventral rostral bones showing variation in patterns of ossifications and presence of foraminae for the efferent branchial arteries; line drawing of Figure 45. Abbreviations found on pages 8–9.

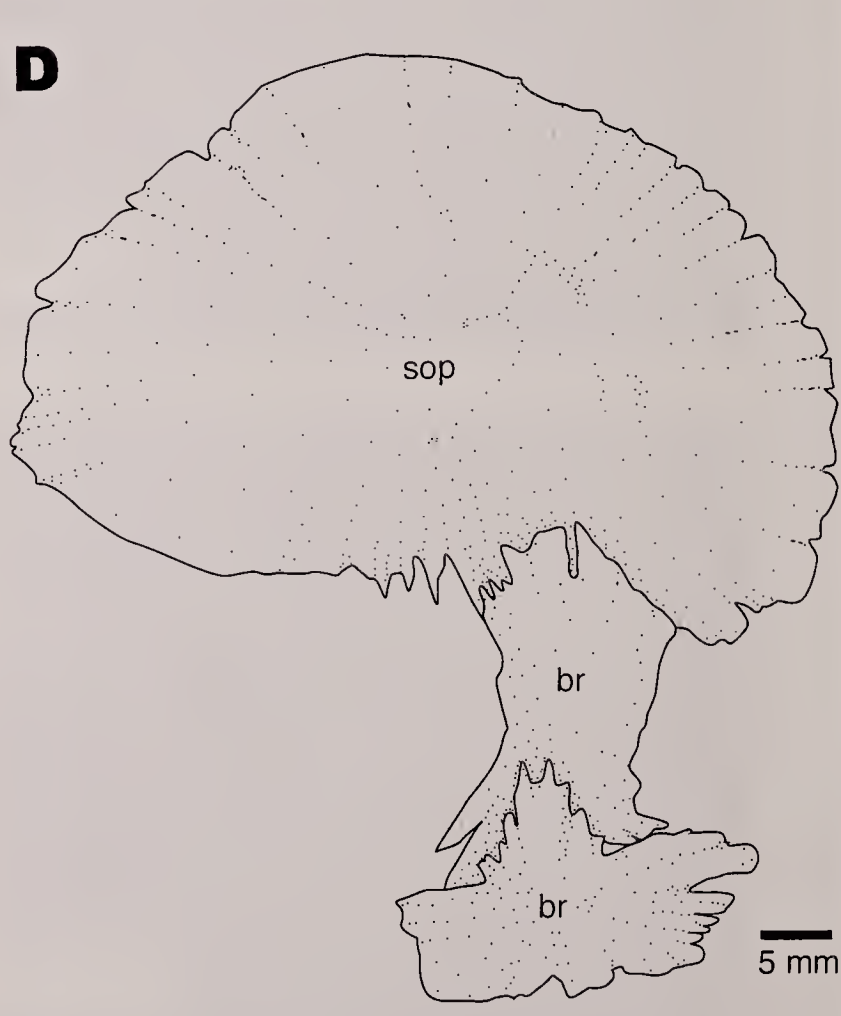


FIG. 47. *Acipenser brevirostrum*, bones of the opercular series, from UMA F10547 (male, 915 mm SL). (**A**) Photograph and (**B**) line drawing of the elements in lateral view. (**C**) Photograph and (**D**) line drawing of the elements in medial view. Anterior to left (images in **C** and **D** reversed to show medial surface of elements in **A** and **B** but with anterior to left). Abbreviations found on pages 8–9.

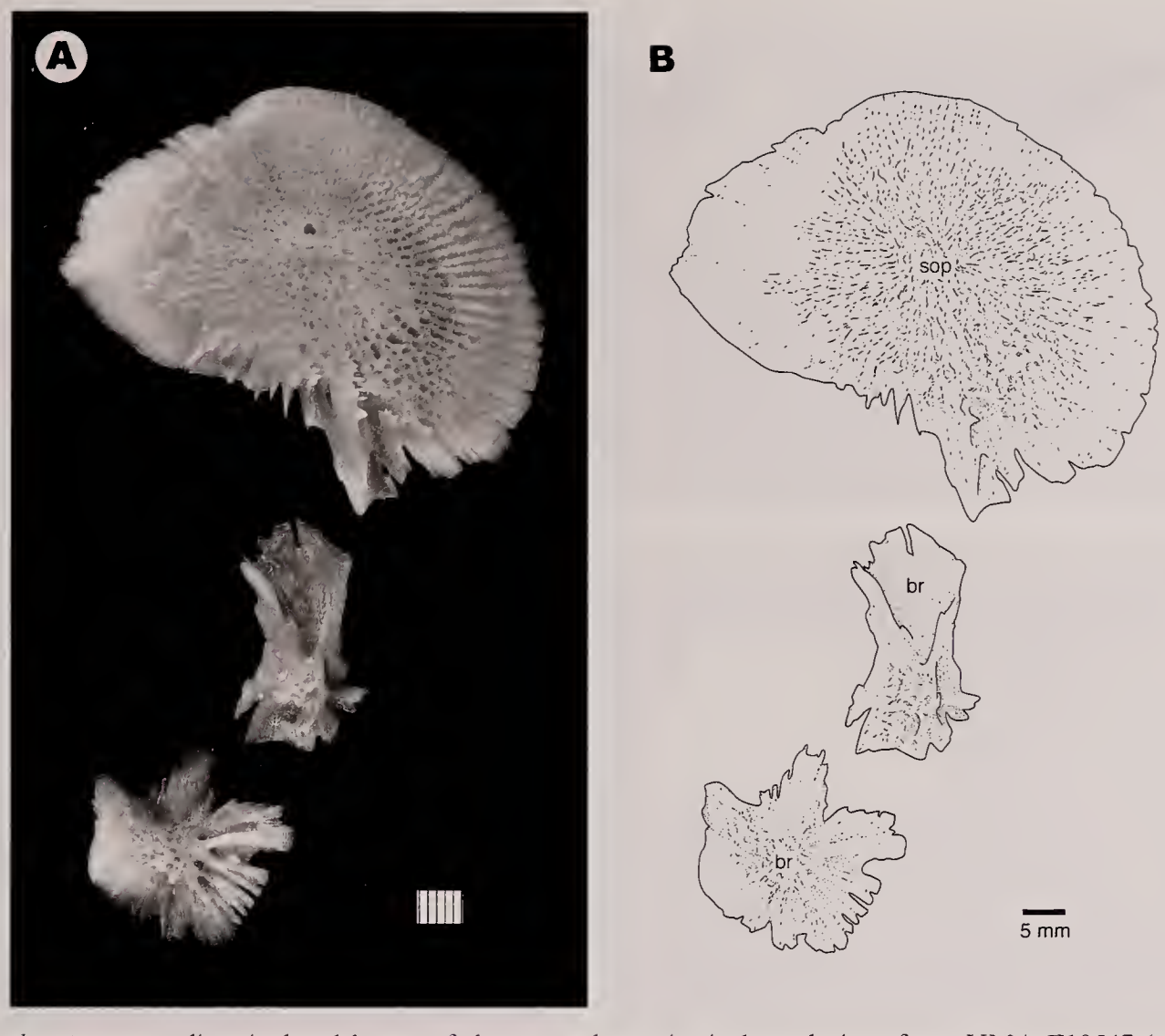


FIG. 48. *Acipenser brevirostrum*, disarticulated bones of the opercular series in lateral view, from UMA F10547 (male, 915 mm SL). (**A**) Photograph and (**B**) line drawing. Anterior to left. Abbreviations found on pages 8–9.

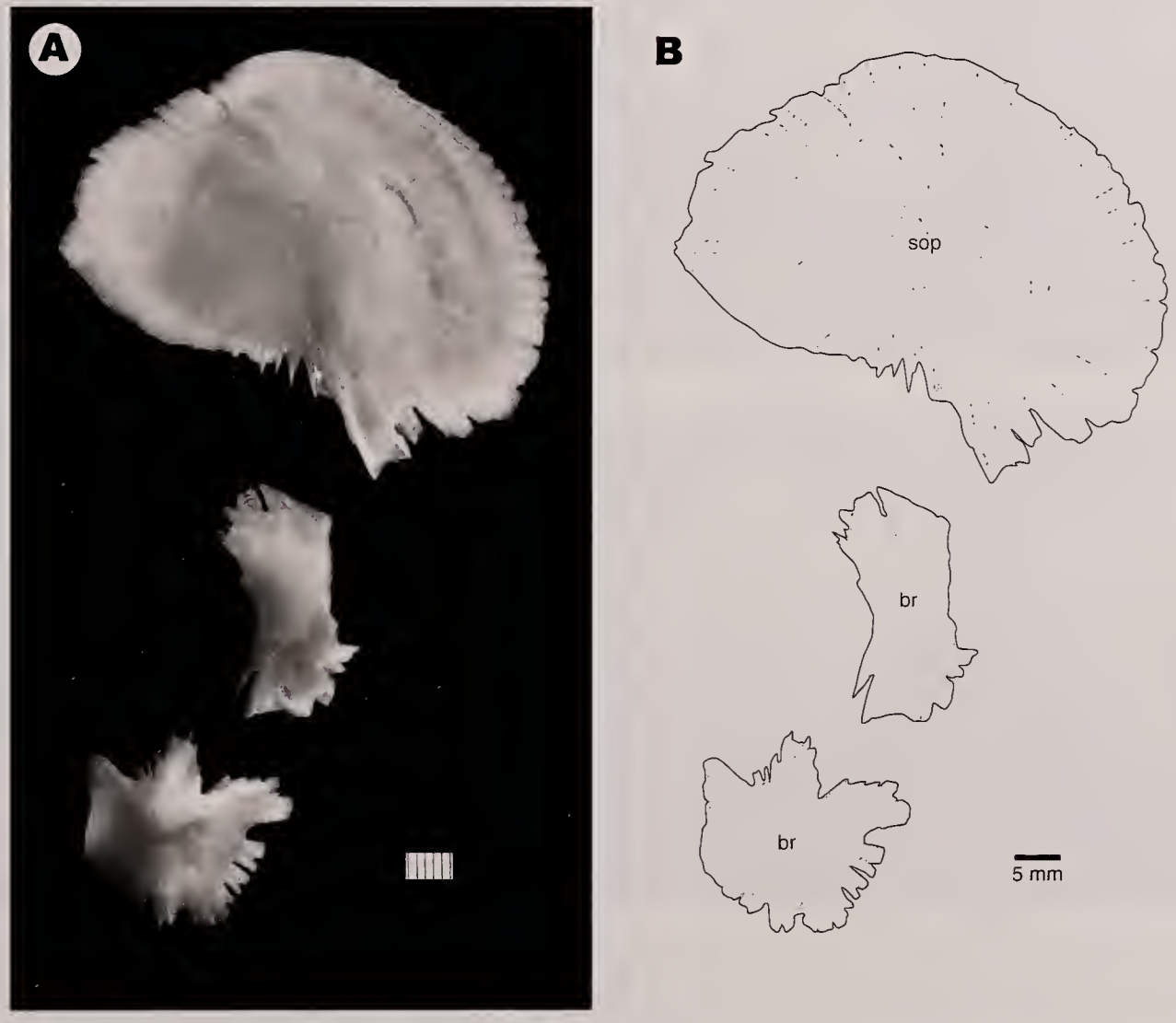


FIG. 49. *Acipenser brevirostrum*, disarticulated bones of the opercular series in medial view, from UMA F10547 (male, 915 mm SL). (**A**) Photograph and (**B**) line drawing. Anterior to left (images reversed). Abbreviations found on pages 8–9.

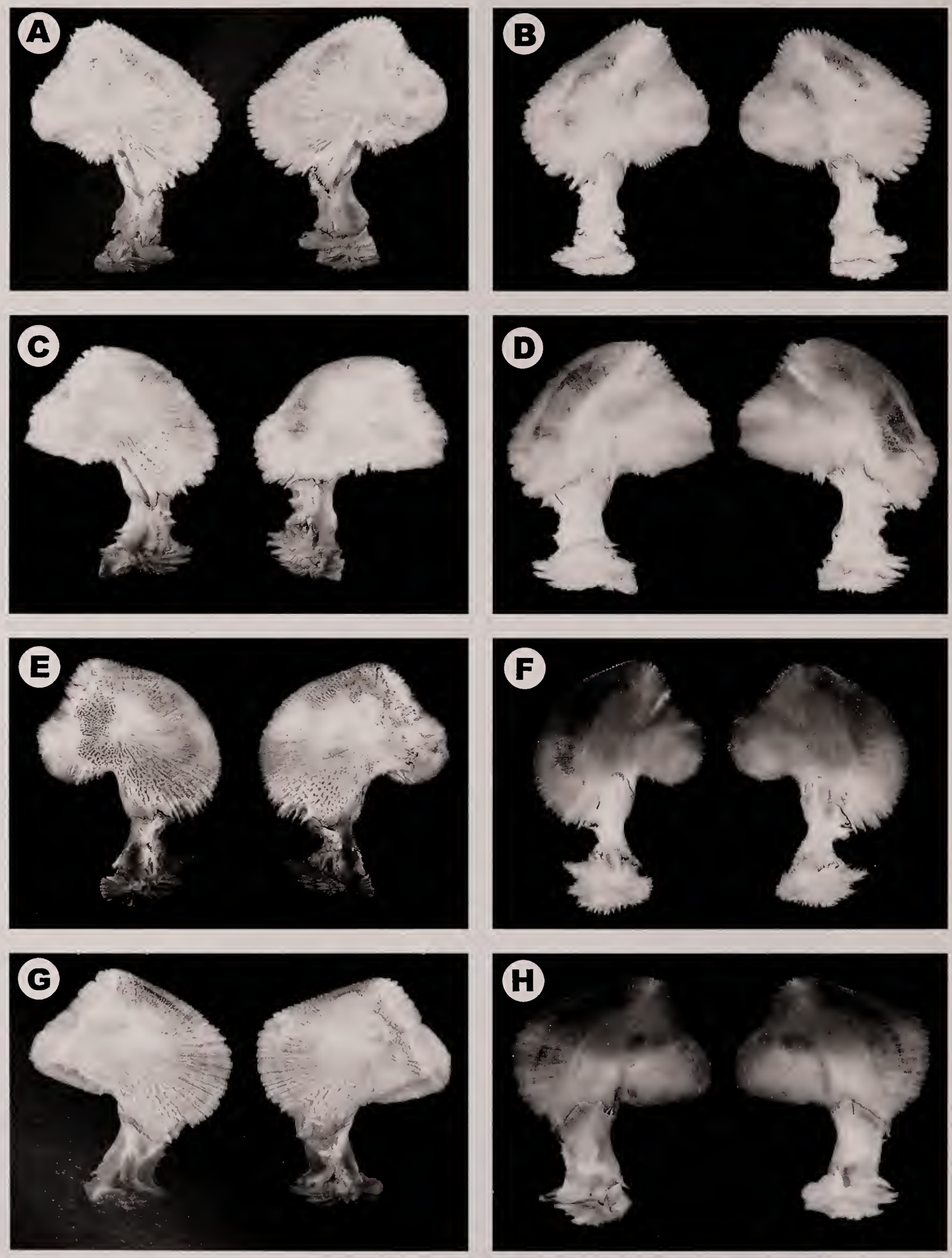


FIG. 50. *Acipenser brevirostrum*, left and right opercular series of four individuals showing variation in shape, number, and form of elements. (**A, B**) UMA F10578 (male, 899 mm SL). (**C, D**) UMA F10431 (male, 930 mm SL). (**E, F**) UMA F10020 (male, 880 mm SL). (**G, H**) UMA F10461 (male, 825 mm SL). Lateral views are shown such that left element has anterior facing left and right element has anterior facing right. Medial views are shown such that left element has anterior facing right and right element has anterior facing left.

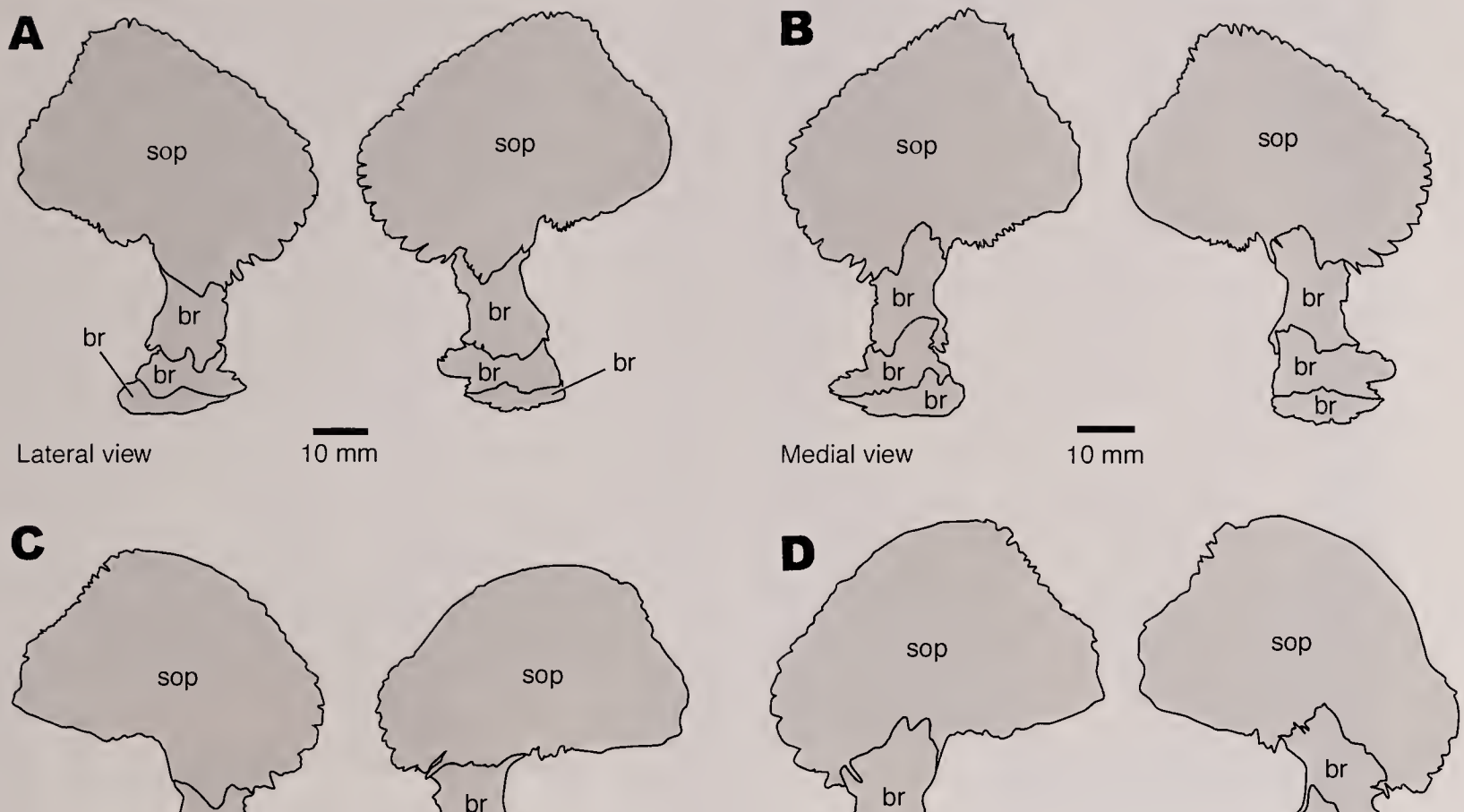


FIG. 51. *Acipenser brevirostrum*, left and right opercular series of four individuals showing variation in shape, number, and form of elements. Line drawing of Figure 50. Abbreviations found on pages 8–9.

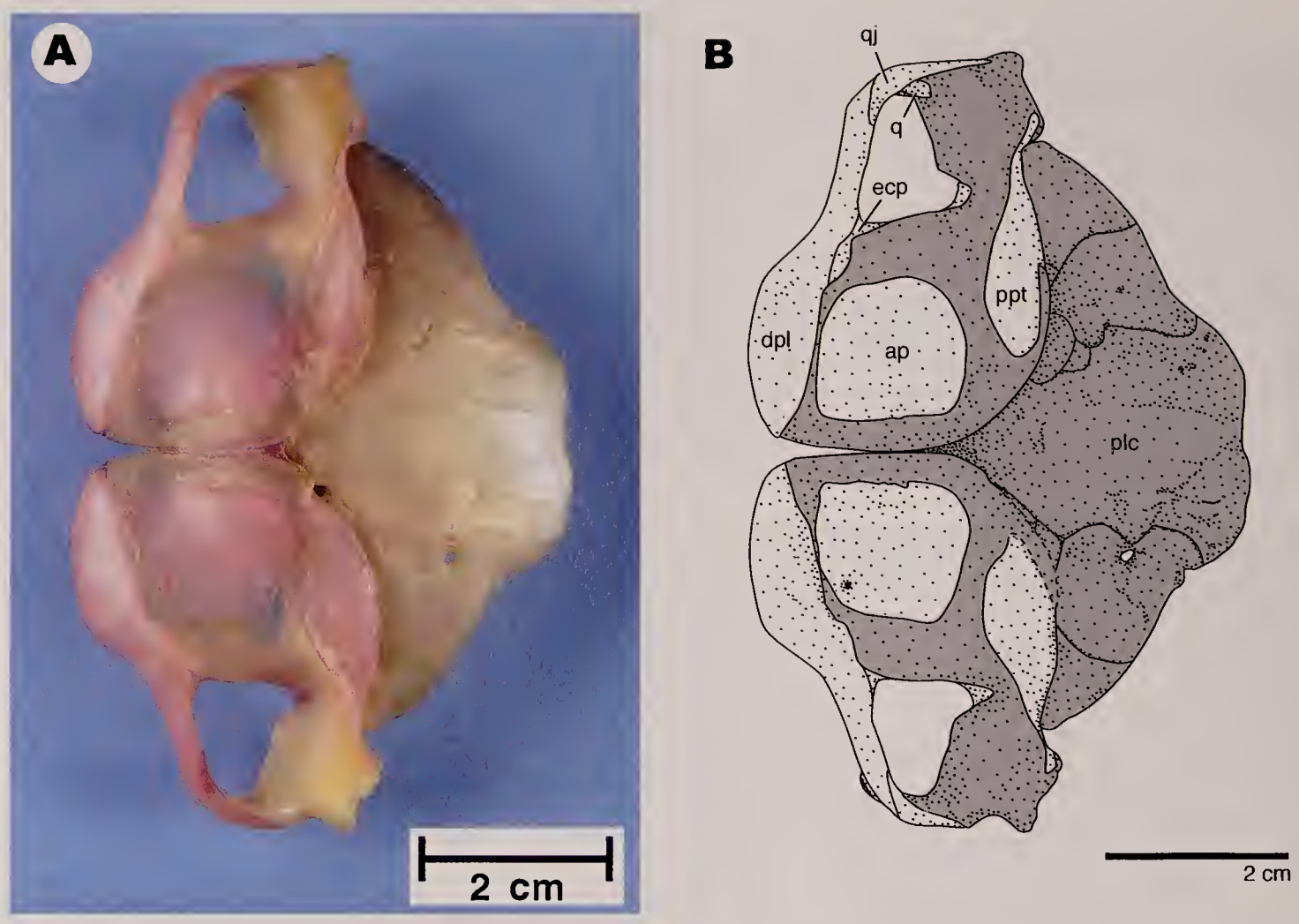


FIG. 52. *Acipenser brevirostrum*, suspensorium in dorsal view, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing. In photo, bone is stained red, and cartilage appears white; in drawing, bone is white, and cartilage is gray. Anterior to left. Abbreviations found on pages 8–9.

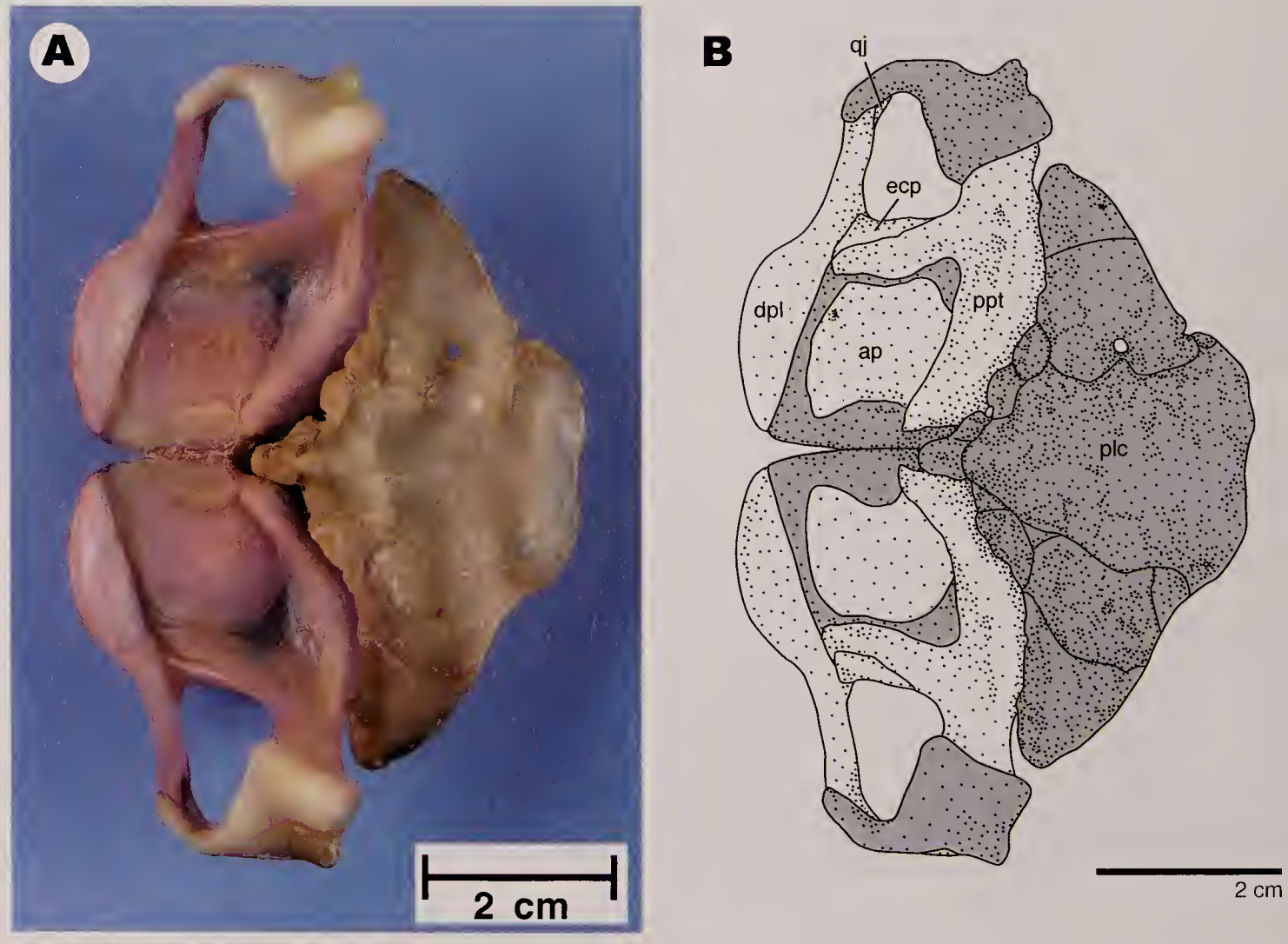
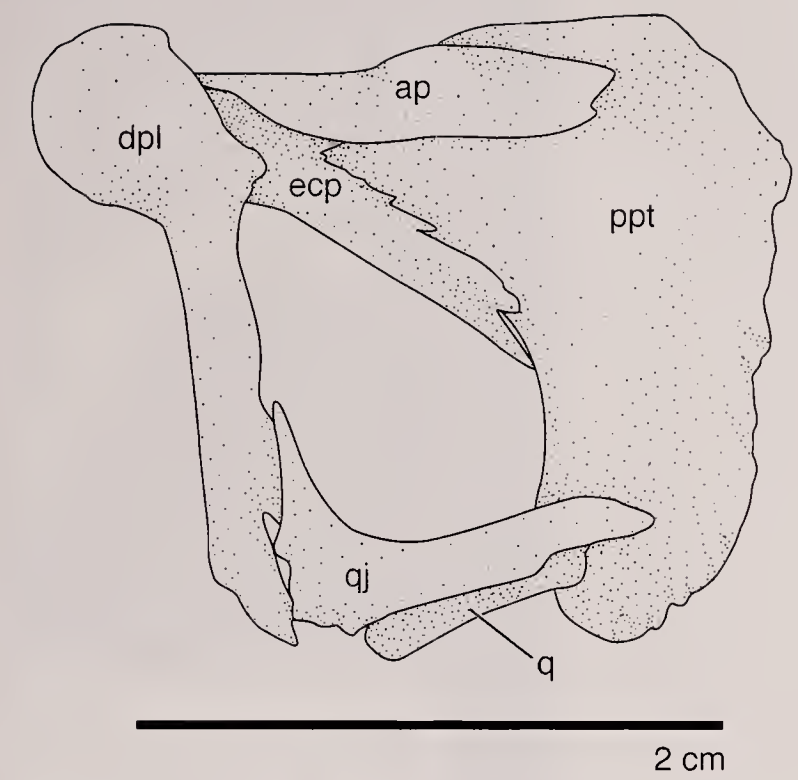


FIG. 53. *Acipenser brevirostrum*, suspensorium in ventral view, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing. In photo, bone is stained red, and cartilage appears white; in drawing, bone is white, and cartilage is gray. Anterior to left. Abbreviations found on pages 8–9.



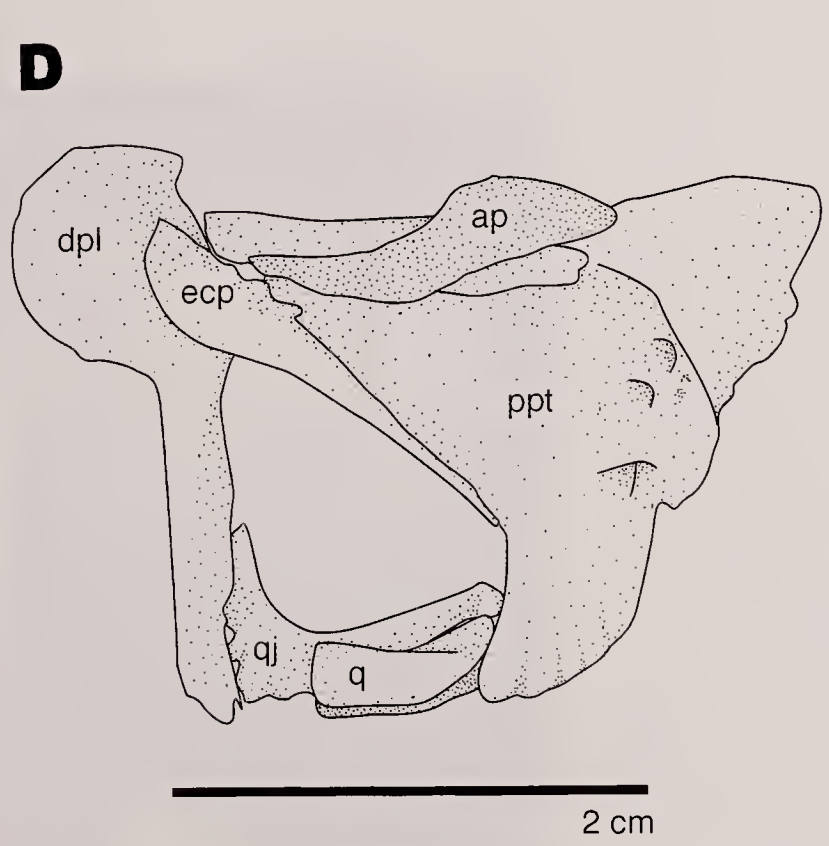


FIG. 54. *Acipenser brevirostrum*, ossifications of the suspensorium, from UMA F10578 (male, 899 mm SL). (**A**) Photograph and (**B**) line drawing of elements in lateral view. (**C**) Photograph and (**D**) line drawing of elements in medial view. Anterior to left (images in **C** and **D** reversed to show medial surface of elements in **A** and **B** but with anterior to left). Abbreviations found on pages 8–9.

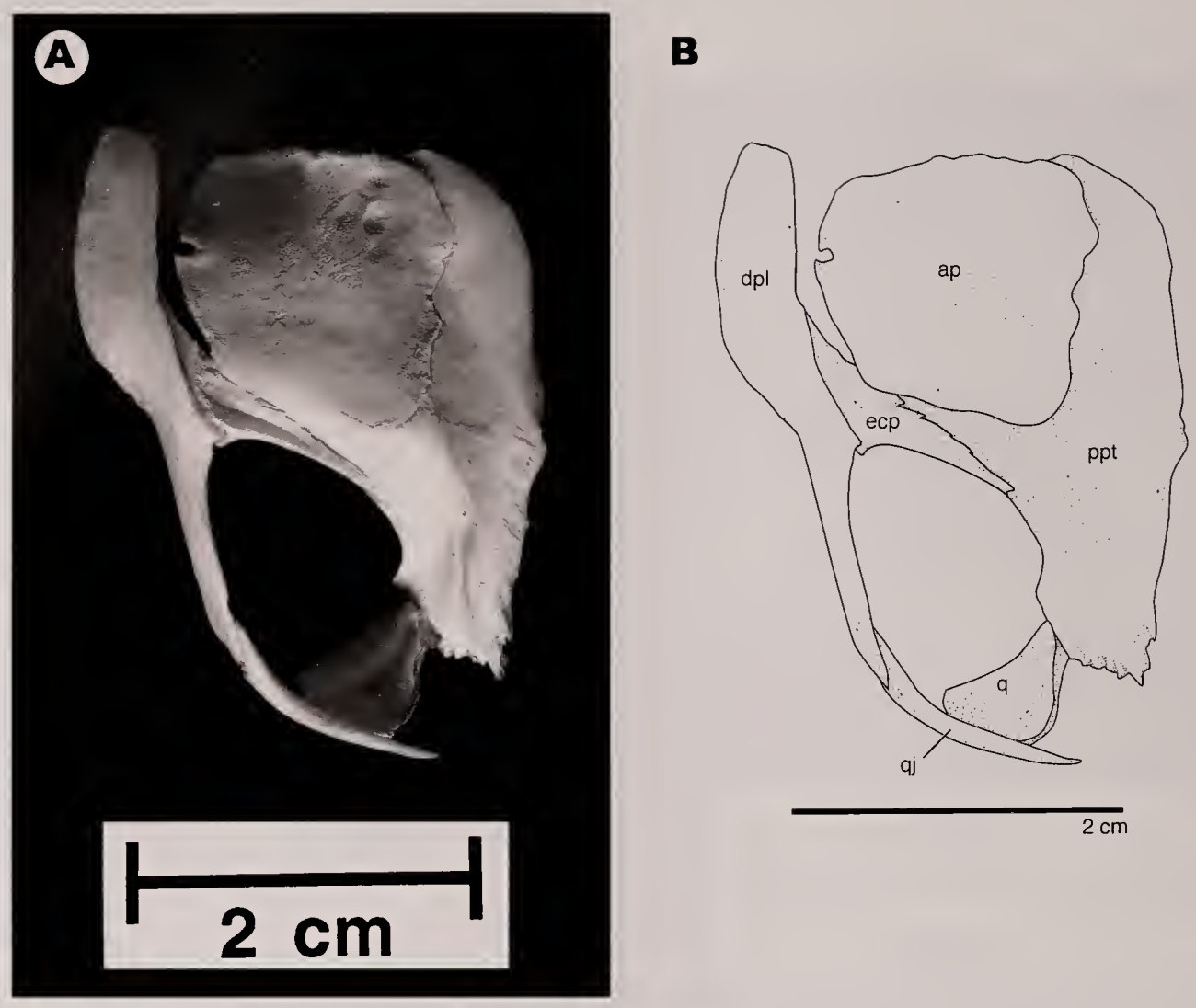


FIG. 55. *Acipenser brevirostrum*, ossifications of the suspensorium in dorsal view, from UMA F10578 (male, 899 mm SL). (**A**) Photograph and (**B**) line drawing. Anterior to left. Abbreviations found on pages 8–9.

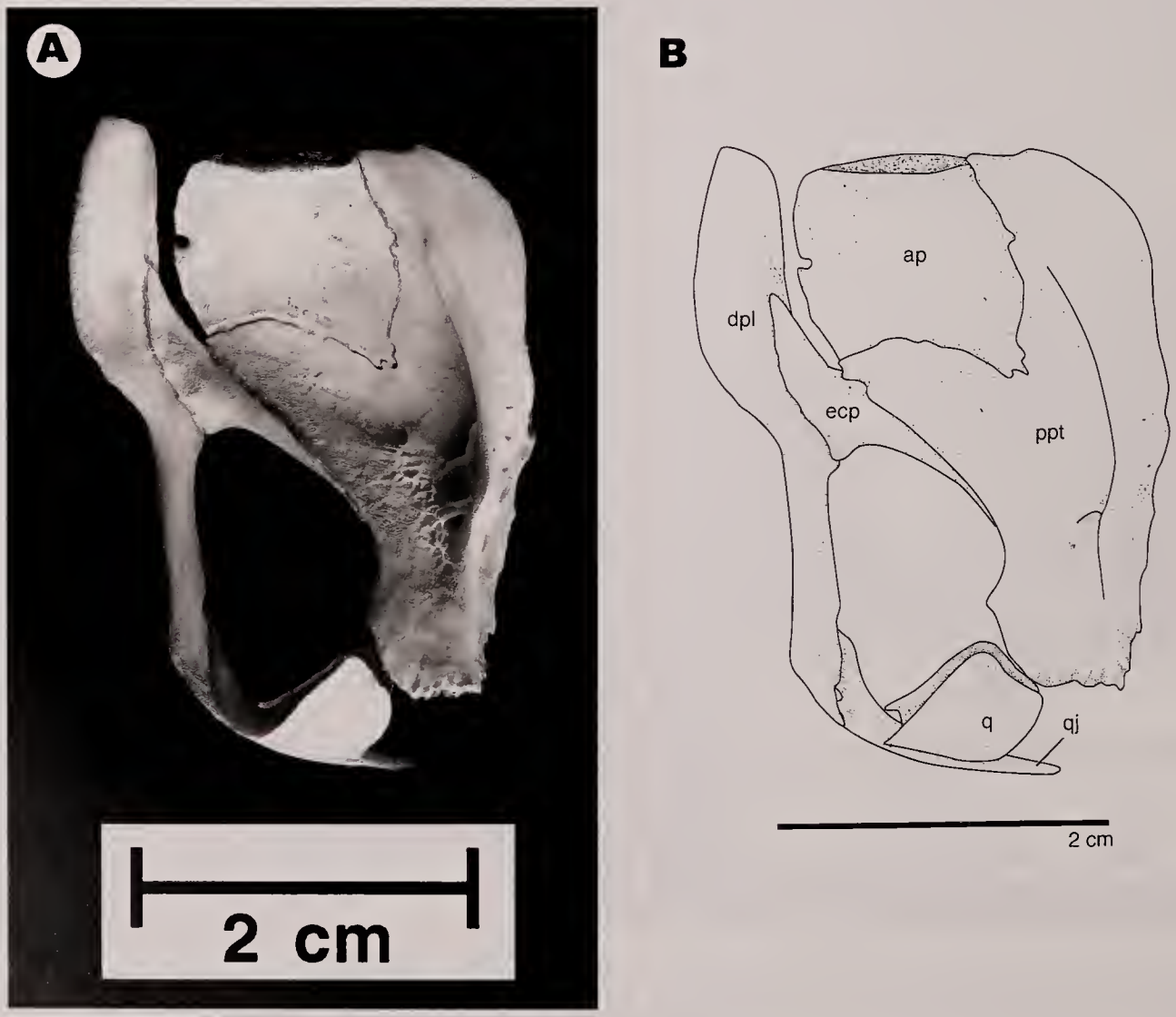
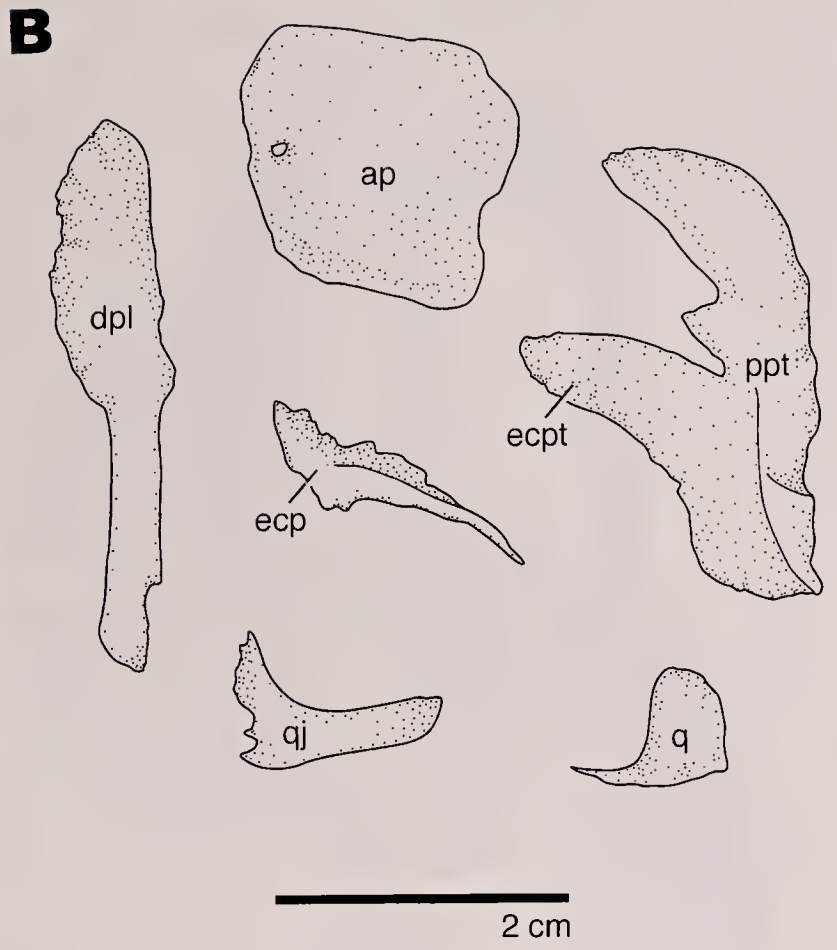


FIG. 56. *Acipenser brevirostrum*, ossifications of the suspensorium in ventral view, from UMA F10578 (male, 899 mm SL). (**A**) Photograph and (**B**) line drawing. Anterior to left. Abbreviations found on pages 8–9.



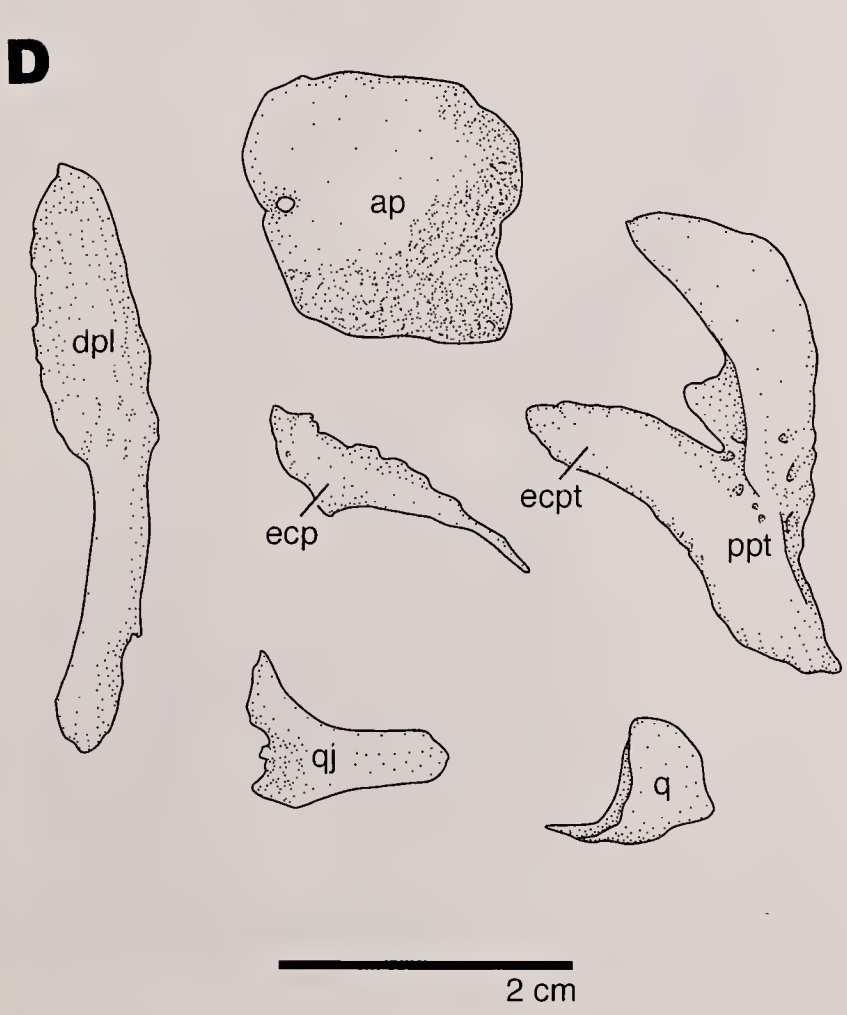


FIG. 57. *Acipenser brevirostrum*, disarticulated bones of the suspensorium, from UMA F10024 (male, 885 mm SL). (**A**) Photograph and (**B**) line drawing of element in dorsal view. (**C**) Photograph and (**D**) line drawing of element in ventral view. Anterior to left. Abbreviations found on pages 8–9.

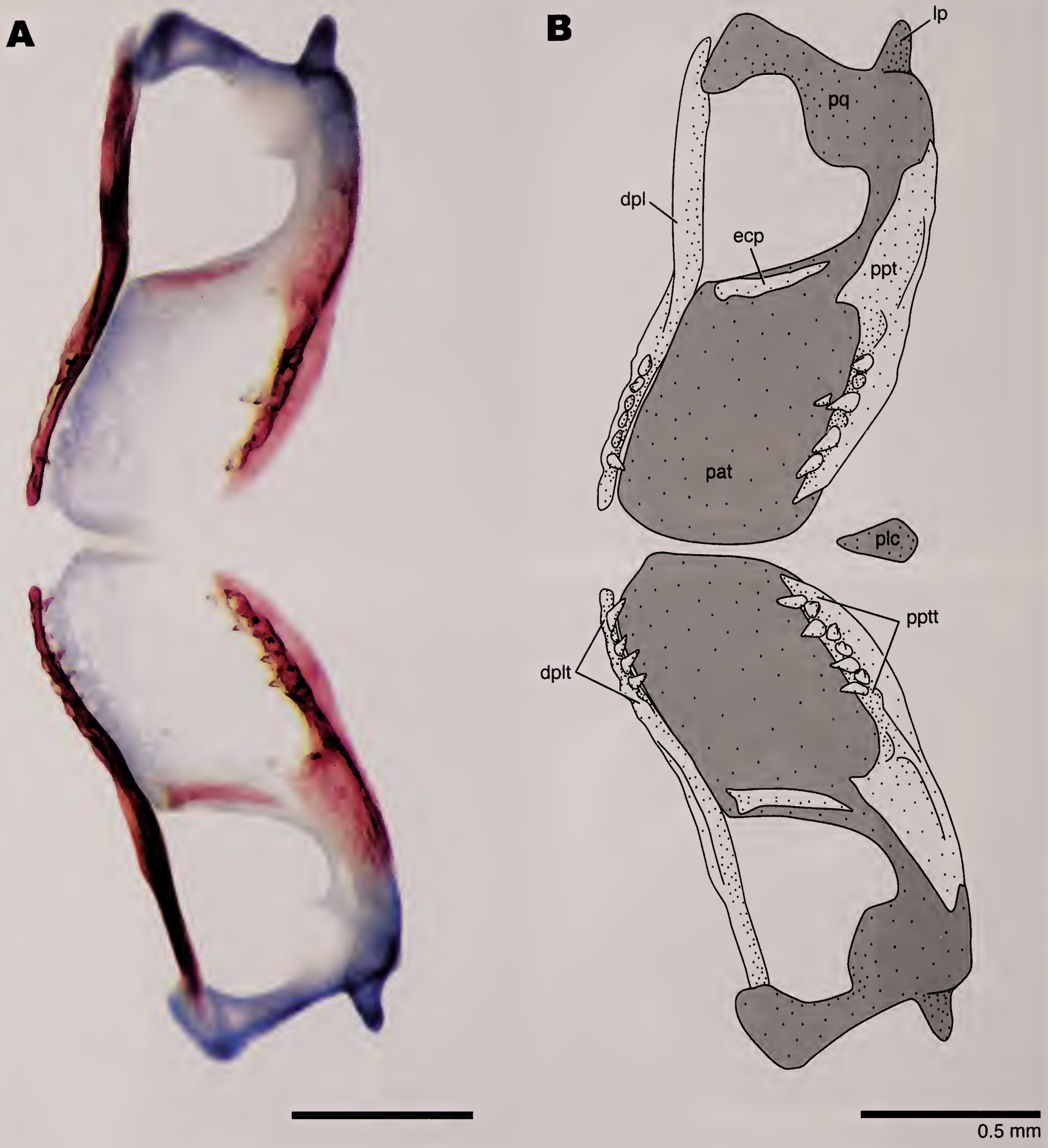


FIG. 58. *Acipenser brevirostrum*, suspensorium at various stages of development. (**A**) Photograph and (**B**) line drawing, from VIMS 12076 (22.1 mm TL). Anterior to left. (**C**) Photograph and (**D**) line drawing, from FMNH 112916 (85.5 mm SL). (**E**) Photograph and (**F**) line drawing, from VIMS 12087 (251 mm SL). Abbreviations found on pages 8–9.

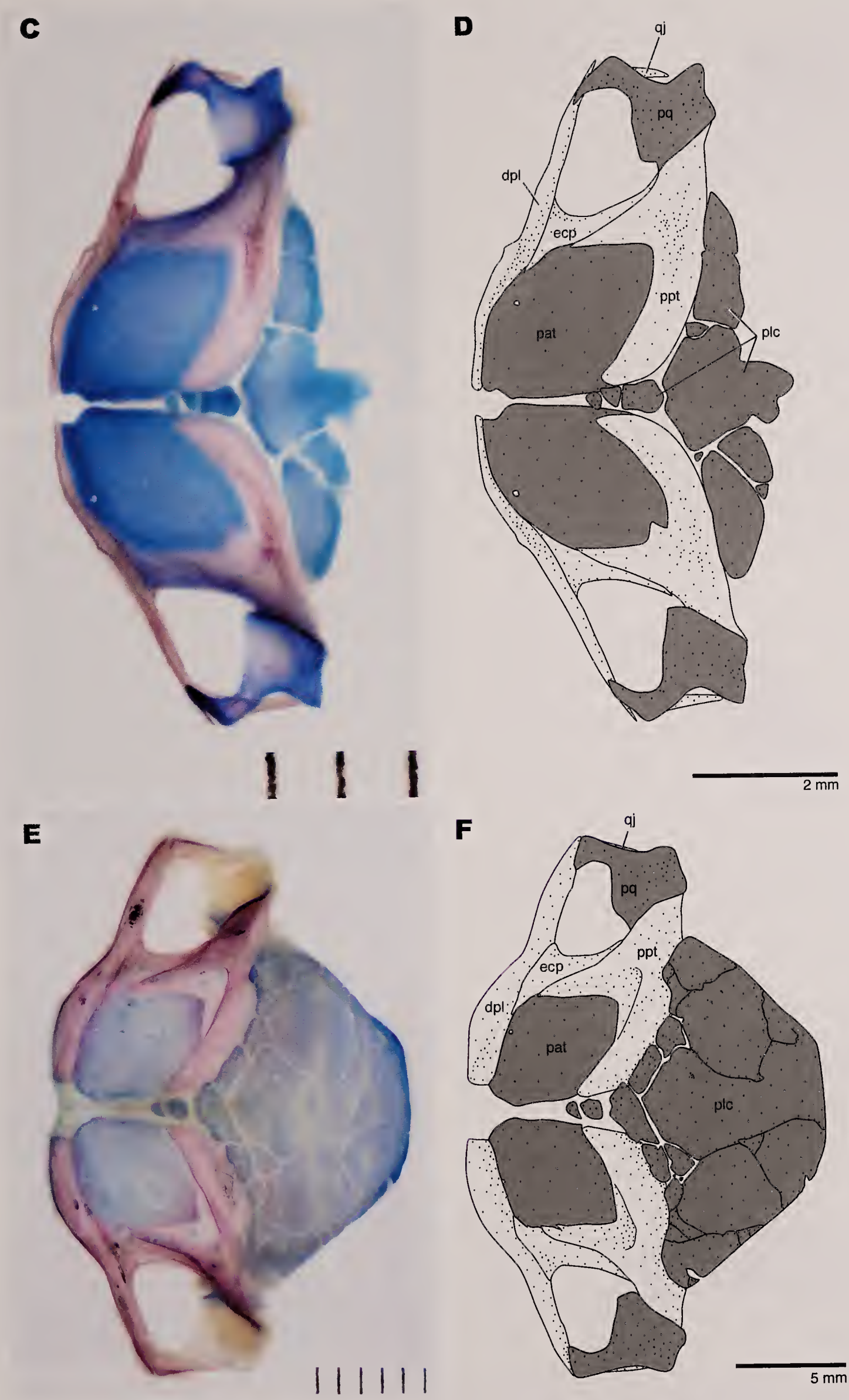


FIG. 58. *Continued.*

TABLE 3. Meristic data and measurements for the head region of a growth series of *Acipenser brevirostrum*.

Specimen no. (SL)	Mouth width (as % SL)	Dentary length (as %SL)	L, R branchiostegals	Prebarbel length (as %SL)
VIMS 12101 (no SL)	3.6 mm (—)	2.3 mm (—)	2, 2	5.0 mm (—)
VIMS 12082 (no SL)	6.2 mm (—)	3.1 mm (—)	3, 3	7.1 mm (—)
FMNH 112215 (50.9 mm)	6.5 mm (13%)	3.2 mm (6%)	2, 3	? (?)
VIMS 12086 (71.1 mm)	6.9 mm (10%)	4.0 mm (6%)	2, 2	11.1 mm (16%)
FMNH 112918 (80.0 mm)	8.7 mm (11%)	4.8 mm (6%)	3, 3	10.8 mm (14%)
FMNH 112916 (85.5 mm)	7.2 mm (8%)	4.9 mm (6%)	2, 2	12.4 mm (15%)
FMNH 112917 (104.3 mm)	9.6 mm (9%)	6.1 mm (6%)	5, 3	13.9 mm (13%)
VIMS 12087 (251 mm)	21.3 mm (8%)	13.9 mm (6%)	3, 3	22.7 mm (9%)
MCZ 54167 (472 mm)	35 mm (7%)	24.0 mm (5%)	2, 2	31 mm (7%)
FMNH 117461 (640 mm)	45 mm (7%)	28.2 mm (4%)	3, 4	36 mm (6%)
ANSP 16953 holotype (690 mm)	? (?)	? (?)	?, ?	18 mm (3%)
FMNH 112212 (710 mm)	44 mm (6%)	29 mm (4%)	3, 2	32 mm (5%)
FMNH 112913 (755 mm)	54 mm (7%)	34 mm (5%)	3, 3	29 mm (4%)
UMA F10578 (899 mm)	60 mm (7%)	34 mm (4%)	3, 3	45 mm (5%)
FMNH 113538 (960 mm)	58 mm (6%)	43 mm (4%)	2, 2	22 mm (2%)

larger sizes did not have an ossified articular (e.g., see Fig. 59). Arratia and Schultze (1991) described a particularly dense region of cartilage in the posterior region of Meckel's cartilage that faces the *pars quadrata*, which might ossify in particularly large or old individuals, such as the one observed here.

Hyoid Arch

The hyoid arch consists of the hyomandibula, the interhyal, the anterior and posterior ceratohyal, and the hypohyal; no symplectic or basihyal elements are present at any stage of development. The hyomandibula of *A. brevirostrum* (**h**, Figs. 26, 35, 36, 64–66) is similar in shape to that of other acipenserids; there are proximal and distal cartilages exposed throughout ontogeny (Figs. 64, 65). The hyomandibula begins ossification at 71 mm TL as a perichondral collar around the narrow shaft of the hyomandibular cartilage. It is unclear if this cartilage represents the hyosymplectic cartilage (as found in other actinopterygians) in which the symplectic does not ossify or if the "symplectic portion" of this cartilage is lost (there is a slight anteroventral elongation in small specimens, e.g., Fig. 66A, B, but this is not clearly a "symplectic region" of a hyosymplectic cartilage). The proximal end of the hyomandibular cartilage is anteroposteriorly squat and articulates with the neurocranium in a distinct ball-and-socket arrangement (see the section Braincase). The distal end of the hyomandibular cartilage forms a laterally compressed blade. This blade rests in an indistinct, shallow depression on the medial surface of the subopercle. In many specimens larger than about 300 mm SL, we discovered irregularly shaped cartilaginous strips on the external surface of the hyomandibula. These external hyomandibular cartilages (**ehc**, Figs. 64, 65, 66E, F) are individually variable in their overall shape and development but are associated with the many struts and ridges found in the middle, constricted portion of the bone.

The robust interhyal (**ihy**, Figs. 26, 35, 36, 38, 64–66) links the ventral portion of the hyomandibula with the palatoquadrate. Its posterior end has dorsal and ventral articulatory surfaces. The dorsal surface articulates with the hyomandibula, whereas the ventral surface articulates with the posterior ceratohyal. Anteriorly, there is a broad articulation with the posterior portion of the lower jaw joint. This element ossifies late in ontogeny, and the bone is still small and restricted to the dorsal edge of the element in the 960 mm SL specimen illustrated in Figure 65 but is further developed in "well-ossified" specimens. The interhyal never shows the sort of rugosity found on other elements of the hyoid and branchial arches (e.g., the hyomandibula and the anterior ceratohyal) but is instead a smooth, perichondral bone. The posteromedial edge of the interhyal also articulates with the posterior ceratohyal. In large adults, the point on the interhyal at which these elements articulate is unossified, leaving a large notch in the bone of the interhyal in medial view.

The anterior and posterior ceratohyals (**cha**, **chp**, respectively; Figs. 26, 35, 36, 38, 67, 68) and the hypohyal (**hh**, Figs. 67, 68) make up the ventral portion of the hyoid arch and form the linkage between the hyomandibula and the gill arches. The posterior ceratohyal is the smaller of the two ceratohyals and is not known to ossify, even in large adults. The posterior ceratohyal articulates with the interhyal (above) and the posteroventral corner of the anterior ceratohyal. The posterodorsal corner of the anterior ceratohyal supports the ventral attachment site for the mandibulohyoid ligament. The anterior ceratohyal is heavily ossified (beginning at 159 mm TL) and is remarkably rugose in large adults. As on the hyomandibula of large specimens, external cartilages are associated with the anterodorsal part of the anterior ceratohyal (**ehyc**, Figs. 67, 68). This element was described as "flat and rectangular" by Findeis (1997, character 20) with asymmetrical mandibulohyoid processes and hypohyal joints, which, taken together, he considered to be a synapomorphy of Acipenseridae. Medial to the anterior ceratohyal is a single hypohyal that never ossifies. The hypohyal contacts the anteriormost extent of the anterior basibranchial copula.

Small, paired tooth plates are associated with the hyoid arch and lie dorsal to the hypohyal and anterior ceratohyal. These appear early in ontogeny (by 17.5 mm TL) but are among the last teeth to disappear (by about 50 mm TL); the adult lacks any pharyngeal tooth plates.

Gill Arches

Gill arches of *Acipenser* have been described and illustrated by many authors (e.g., Parker, 1882; Stengel, 1962; Nelson, 1968, 1969). There are commonly two basibranchial copulae in

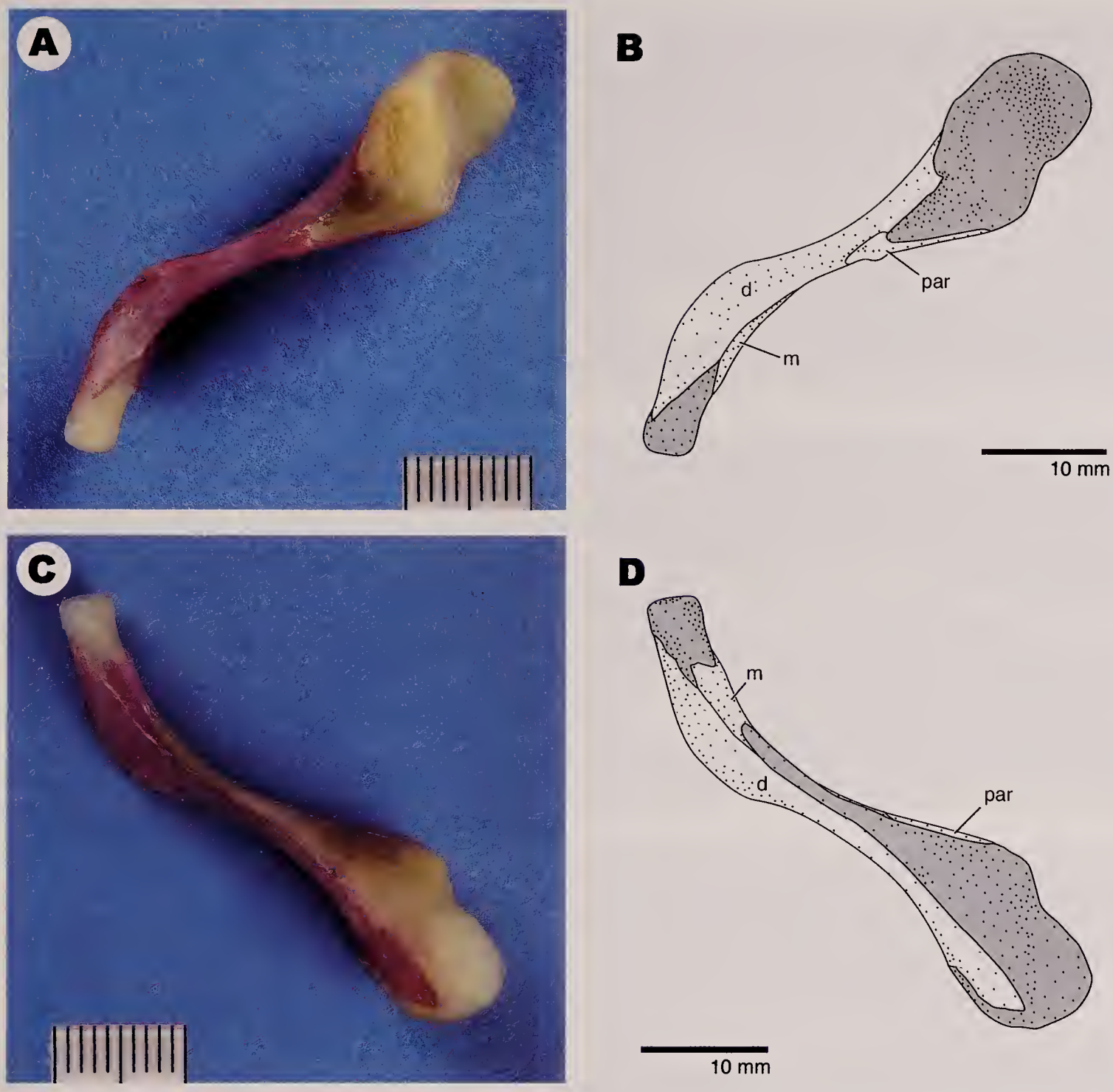


FIG. 59. *Acipenser brevirostrum*, lower jaw, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing of elements in dorsal view. (**C**) Photograph and (**D**) line drawing of elements in ventral view. In photo, bone is stained red, and cartilage appears white; in drawing, bone is white, and cartilage is gray. Anterior to left. Abbreviations found on pages 8–9.

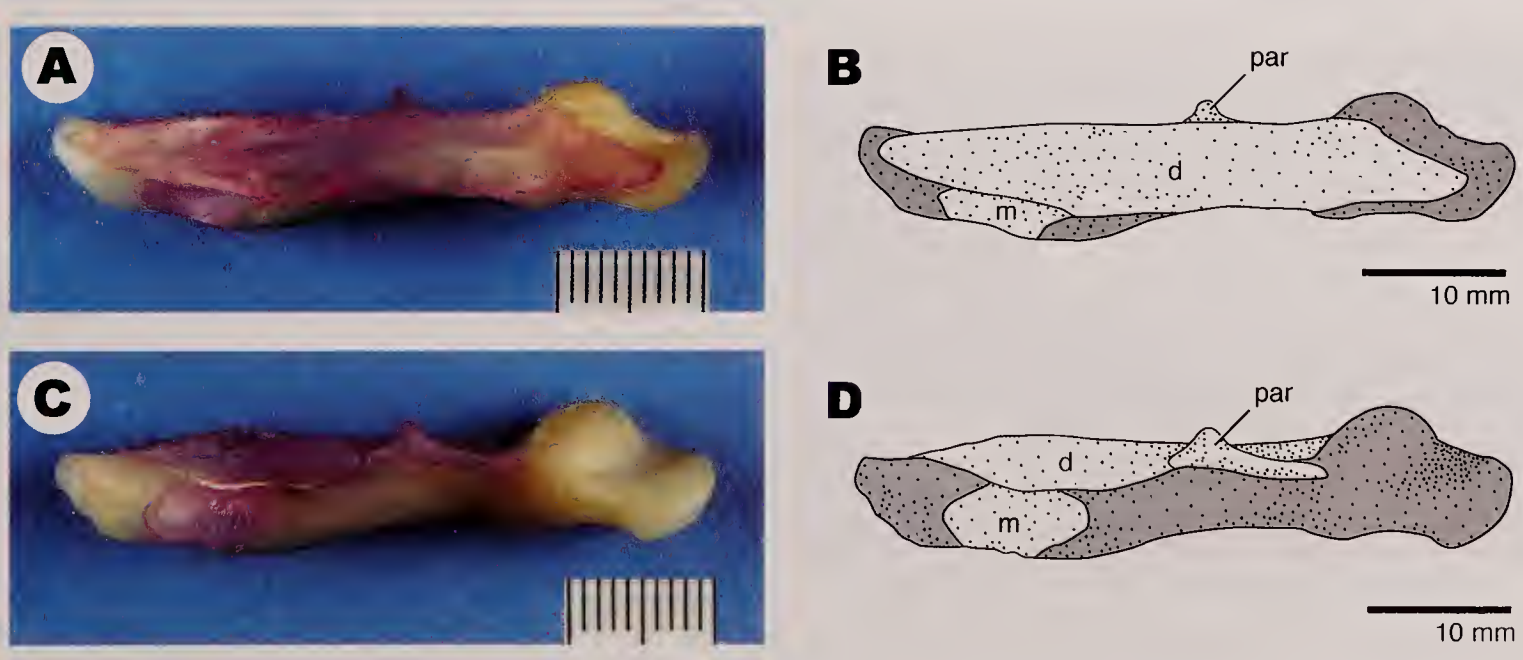
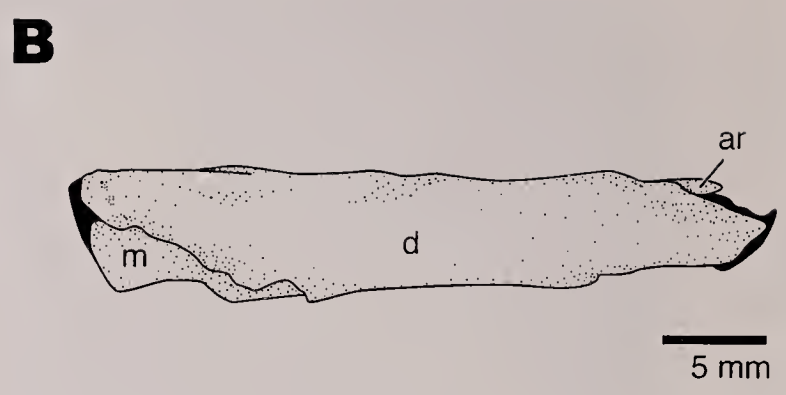
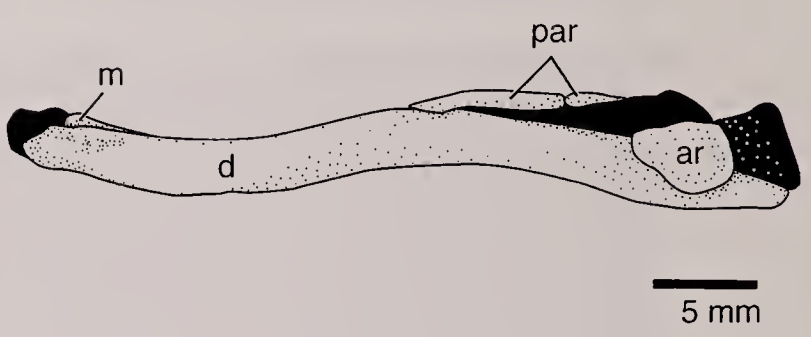
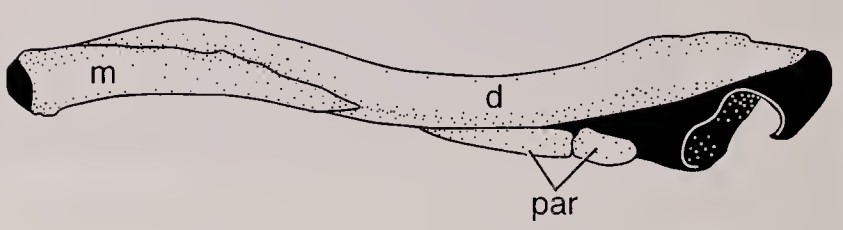


FIG. 60. *Acipenser brevirostrum*, lower jaw, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing of elements in lateral view. (**C**) Photograph and (**D**) line drawing of elements in medial view. In photo, bone is stained red, and cartilage appears white; in drawing, bone is white, and cartilage is gray. Anterior to left (images in **C** and **D** reversed to show medial surface of elements in **A** and **B** but with anterior to left). Abbreviations found on pages 8–9.







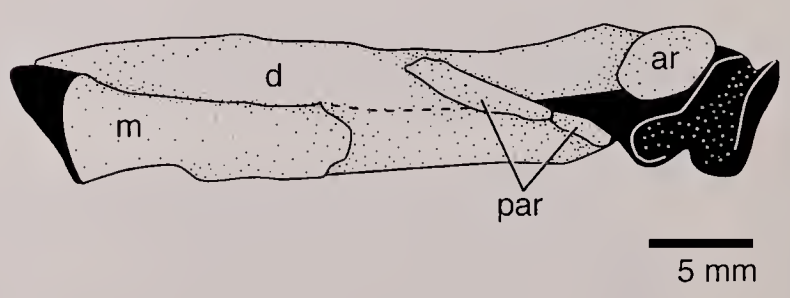


FIG. 61. *Acipenser brevirostrum*, ossifications of the lower jaw, from UMA F10578 (male, 899 mm SL). (**A**) Photograph and (**B**) line drawing of elements in lateral view. (**C**) Photograph and (**D**) line drawing of elements in dorsal view. (**E**) Photograph and (**F**) line drawing of elements in ventral view. (**G**) Photograph and (**H**) line drawing of elements in medial view. Dashed line in **H** indicates position of Meckel's cartilage. Cartilage shown in black; note that cartilages are dried and somewhat distorted in this preparation. Scale bar in photographs in millimeters. Anterior to left (images in **G** and **H** reversed to show medial surface of elements but with anterior to left). Abbreviations found on pages 8–9.

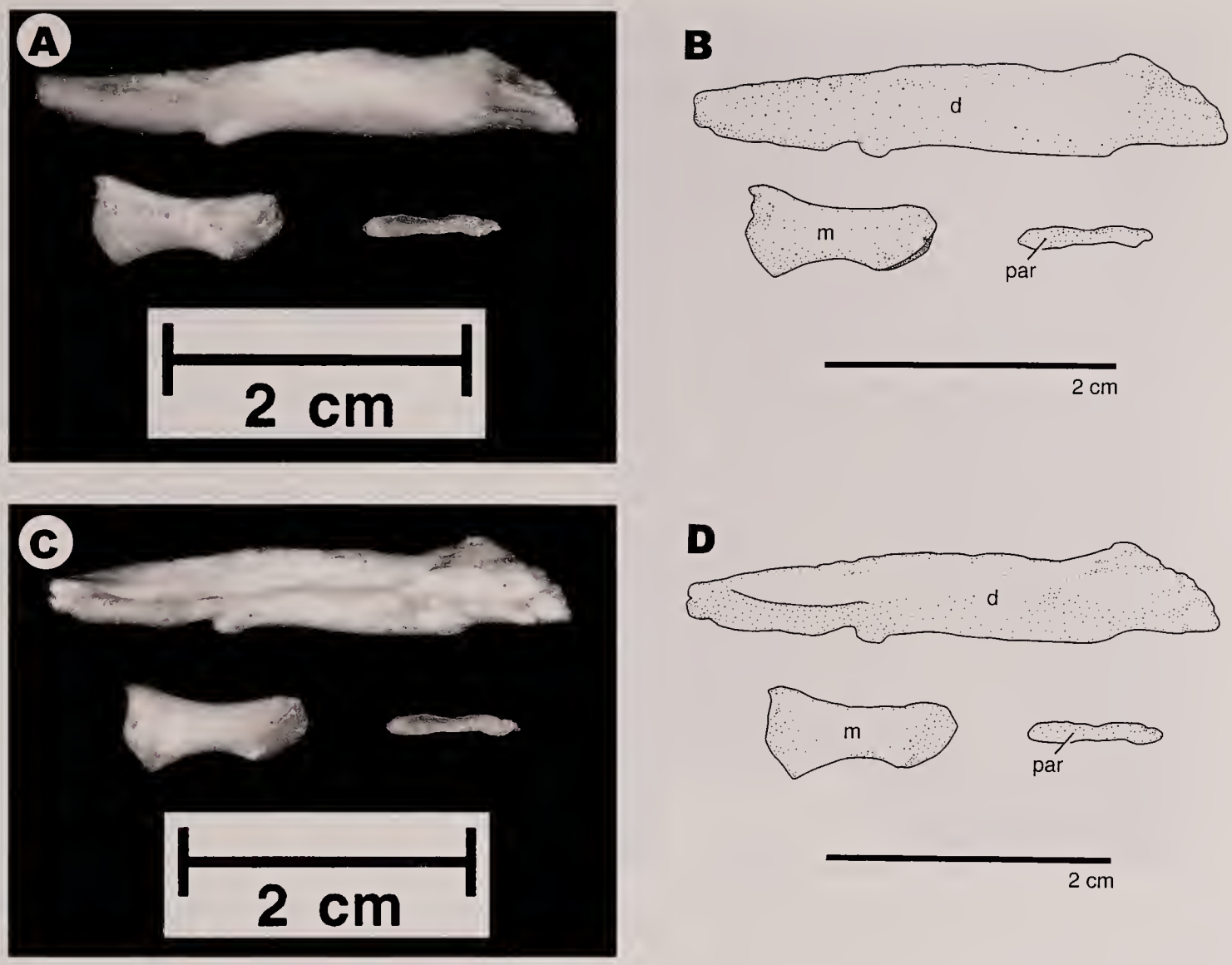


FIG. 62. *Acipenser brevirostrum*, ossifications of the lower jaw, from UMA F10024 (sex unknown, 880 mm SL estimated). (**A**) Photograph and (**B**) line drawing of elements in lateral view. (**C**) Photograph and (**D**) line drawing of elements in medial view. Note that the articular was not ossified in this specimen. Scale bar in photographs in millimeters. Anterior to left (images in **C** and **D** reversed to show medial surface of elements but with anterior to left). Abbreviations found on pages 8–9.

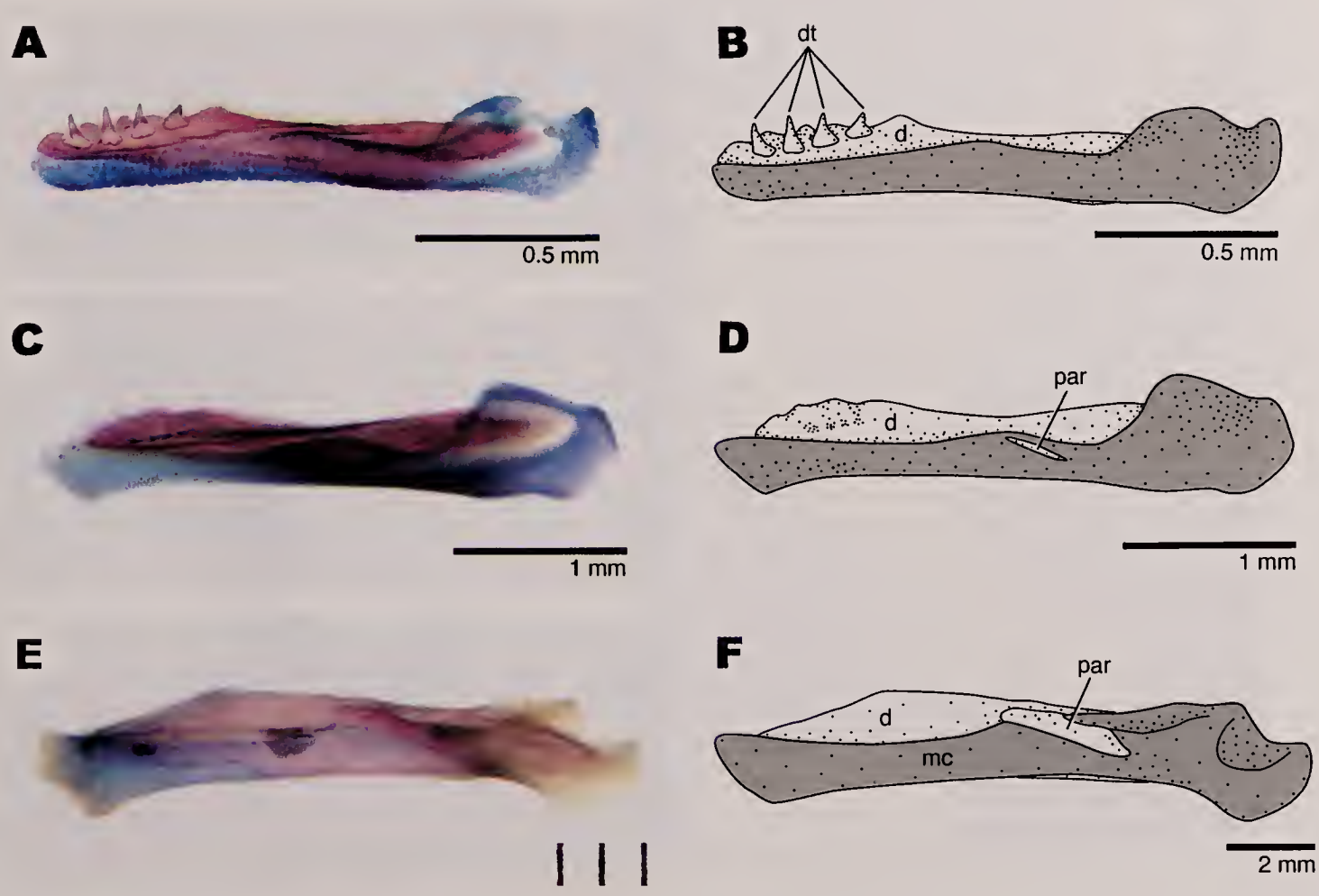


FIG. 63. *Acipenser brevirostrum*, lower jaw at various stages of development, in medial view. (**A, B**) VIMS 12076, 22.1 mm TL. (**C, D**) VIMS 12082, 58.5 mm TL. (**E, F**) VIMS 12087, 251 mm SL. Anterior to left. Abbreviations found on pages 8–9.

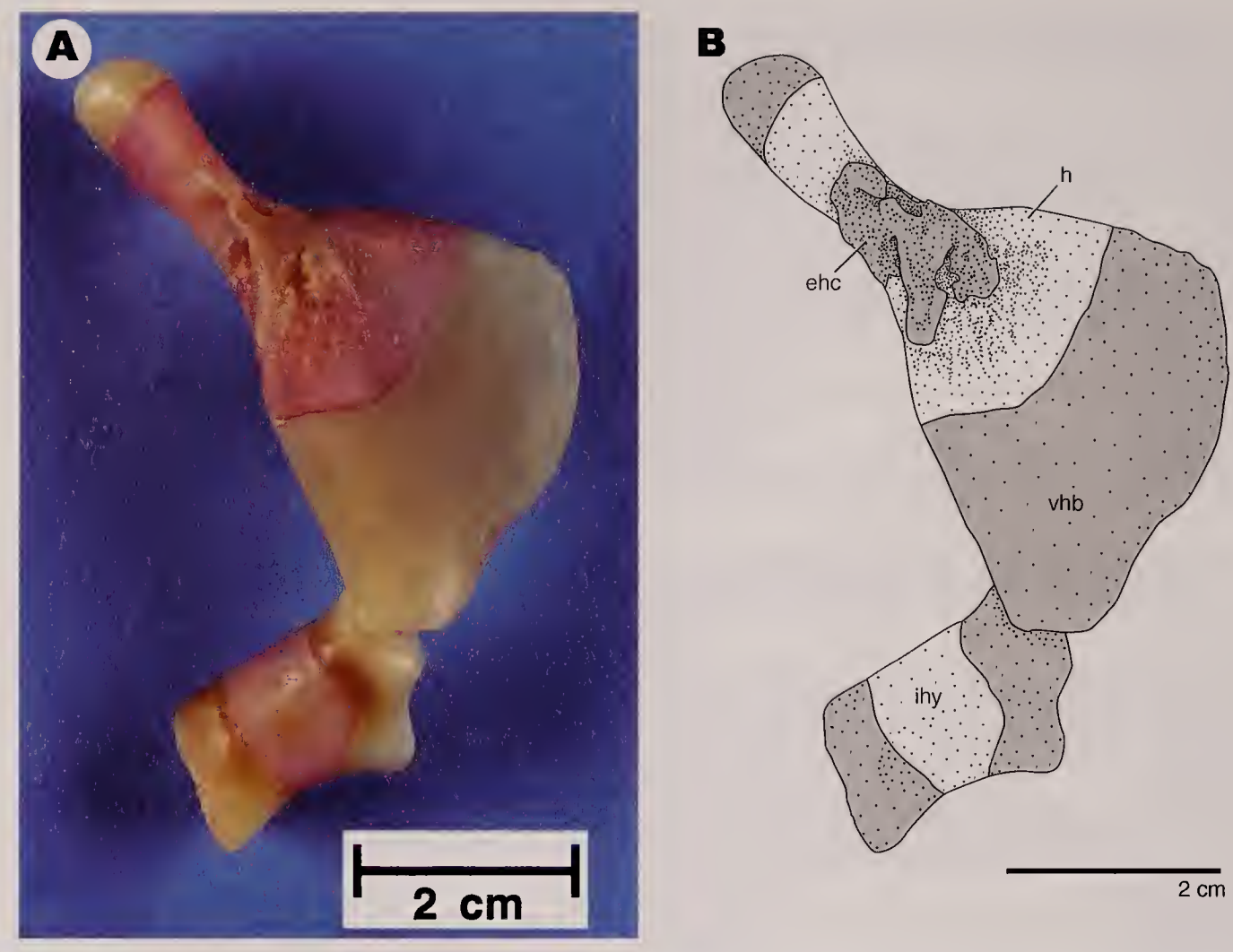


FIG. 64. *Acipenser brevirostrum*, dorsal portion of the hyoid arch in lateral view, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing. In photo, bone is stained red, and cartilage appears white; in drawing, bone is white, and cartilage is gray. Anterior to left. Abbreviations found on pages 8–9.

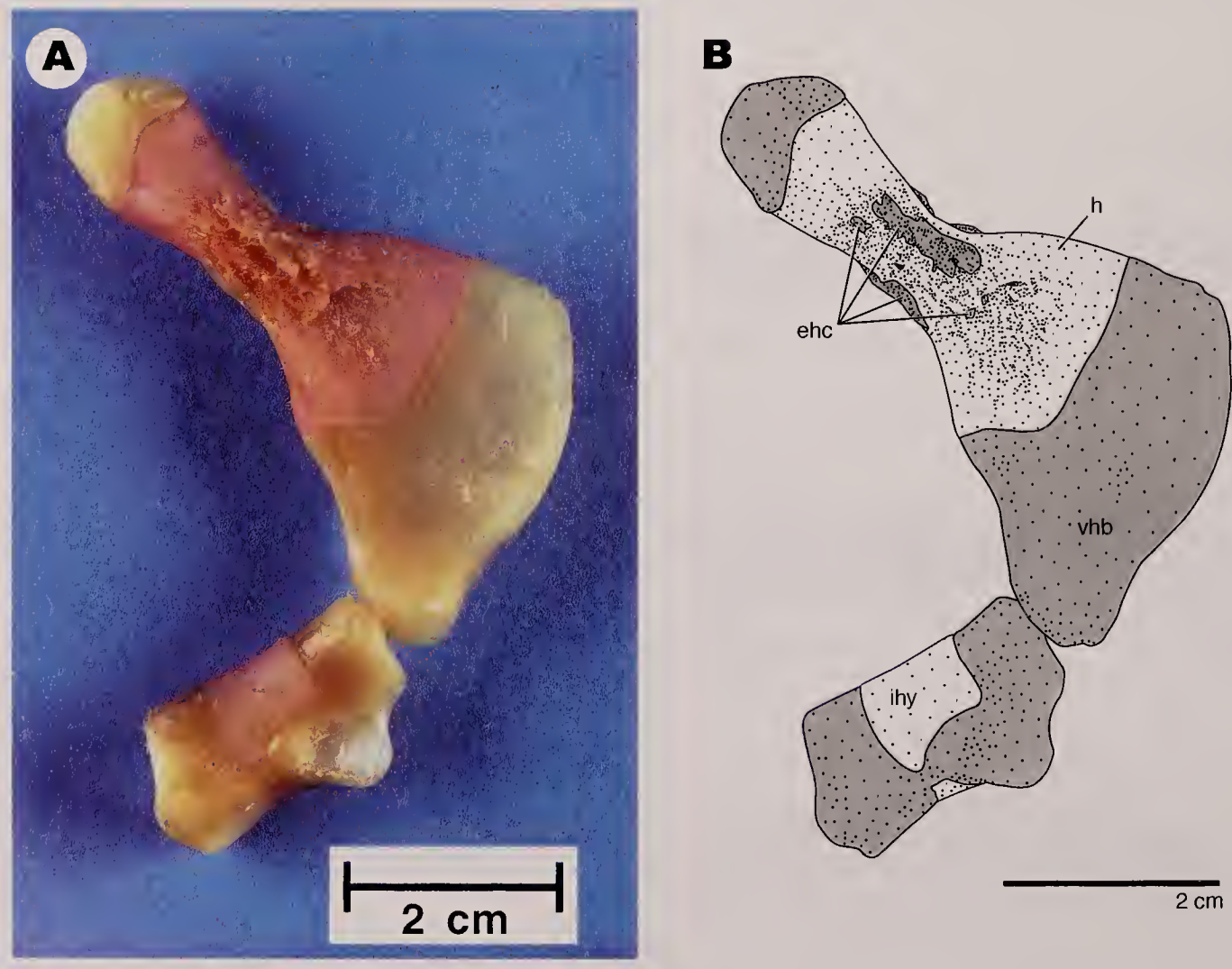


FIG. 65. *Acipenser brevirostrum*, dorsal portion of the hyoid arch in medial view, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing. In photo, bone is stained red, and cartilage appears white; in drawing, bone is white, and cartilage is gray. Anterior to left. Abbreviations found on pages 8–9.

A. brevirostrum (**bbc**, Figs. 71, 72). The anterior copula is the largest and is contacted by the left and right hypohyals and hypobranchials 1, 2, and 3. The more posterior copula(e) is much smaller. The number of basibranchial copulae is apparently variable among species of Acipenseridae, although some of this variation may be ontogenetic or individual. For instance, Findeis (1997) illustrated three in *Huso* (also in the polyodontid *Psephurus*) and two in *Scaphirhynchus*. Parker (1882, pl. 18, fig. 10) illustrated four copulae in an adult *A. sturio*; he found a single element present in a small juvenile specimen (his pl. 16, figs. 4, 5) and in a larval specimen of *A. ruthenus*, (his pl. 13, fig. 12, and pl. 14, fig. 5). For *A. ruthenus*, Sewertzoff (1928, pl. 7, figs. 26–28) illustrated three larvae: the smaller two individuals have a single chondrified basibranchial, and the largest has two copulae; Stengel (1962, figs. 12, 13) showed three and two copulae, respectively, in his specimens of *A. ruthenus* (ontogenetic stage is unknown). Van Wighe (1882, cited by Nelson, 1969) illustrated two ossifications (basibranchials 4 and 5 according to Nelson, 1969) in his description of the gill arches of *Acipenser*. However, we did not find basibranchial ossifications in any of our specimens of *A. brevirostrum*, even in the largest specimens examined, and regard Van Wighe's report as erroneous or based on an anomalous specimen.

A thin, elongate cartilaginous element lies between the left and right fifth ceratobranchials posterior to the basibranchial series in most specimens of *A. brevirostrum* that we examined. This element (**uga**, Figs. 71, 72E, F) was referred to as an "unnamed" or "unidentified" median cartilage by Grande and Bemis (1991) and Findeis (1997, fig. 13), although it is possible that it represents a posterior basibranchial copula. The absence of this element was considered to be a synapomorphy of all Acipenseridae to the exclusion of *Huso* by Findeis (1997, character 37; i.e., his "Acipenserinae"), although we reject this conclusion because we found this element in both juvenile and adult specimens of *A. brevirostrum* as well as in most other specimens of *Acipenser* we examined (for which this region was suitably prepared).

The hypobranchial series of *A. brevirostrum* generally consists of three elements (**hb1–3**, Figs. 71, 72); a fourth hypobranchial is variably present as an autogenous element (**hb4**, Fig. 72E, F). The anteriormost is the largest, and the elements become progressively smaller posteriorly. The first hypobranchial is a large element with a flat dorsal surface and prominent anterolateral process; hb1 bears a foramen in its anterior surface. The third hypobranchial bears dorsal and ventral median processes. The left and right hb3 meet in the midline between the two basibranchial copulae, contacting with both elements. When present, the left and right hb4 contact each other dorsally in the midline, but extend forward ventrally to contact the ventral part of the posterior basibranchial copulae (this is the form of the proximal portion of certatobranchial 4 when hb4 is not present; Figs. 71, 72A–D). Hypobranchals 1 and 2 were found to be perichondrally ossified in large adult specimens (e.g., FMNH 113538, 960 mm SL).

There are five ceratobranchials (**cb1–5**, Figs. 69D, 70–72) in *A. brevirostrum*. All certatobranchials are ossified and are deeply concave ventrally, forming a trough for the branchial blood vessels. As with other series of elements of the branchial arches, the anterior elements are larger and more robust than are the more posterior elements in the series. The proximal cartilaginous ends of cb5 are enlarged flat structures that are oriented nearly vertically.

The dorsal portion of the gill arches of *A. brevirostrum*, as those of acipenserids generally (see Nelson, 1968, fig. 4B), are composed of elements in three distinct series: the epibranchials, infrapharyngobranchials, and suprapharyngobranchials. Four epibranchials (**eb1–4**, Figs. 73, 74) lie in series with the ceratobranchials 1–4. All four epibranchials are ossified in adults and are deeply concave dorsally, where they support the branchial blood vessels. Epibranchial 4 is a relatively flat, largely cartilaginous element that is perforated by several small foramina (Fig. 73).

Three elements form the infrapharyngobranchial series (**iph1–3**, Figs. 73, 74), and these lie in series with eb1–3. The first two infrapharyngobranchials are ossified in adults, but the bone does not show the rugosity of other branchial ossifications (e.g., the ceratobranchials and anterior epibranchials). Two suprapharyngobranchials (**sph1–2**, Figs. 73, 74) are associated with the first two gill arches. These elements are entirely cartilaginous, even in large adults.

The gill rakers (**gr**, Figs. 72, 74) of *A. brevirostrum* are thin triangular elements that line the leading and trailing edges of each gill arch (Figs. 69, 70). The base of each gill raker is roughly teardrop shaped, with the tapered end directed away from the supporting gill arch element. The ossified portions of the gill rakers are deeply embedded in the thick dermis covering the entire gill arch and are easily separated from the skeleton of the gill arch (they are frequently removed with the soft tissue and are missing from dry skeletal preparations). No denticles are associated with the gill rakers in sturgeons. The gill rakers of sturgeons vary in overall form (see Findeis, 1997, fig. 25). For instance, those of *Scaphirhynchus* and *Pseudoscaphirhynchus* arc crenulated and sharply pointed, respectively; these conditions were considered to be synapomorphies for each genus by Findeis (1997, characters 58, 63).

The large pseudobranch (not illustrated) is situated in a shallow concavity along the posterior margin of the subopercle.

Vertebral Column

The vertebral column of Acipenseriformes has been described by Gadow and Abbot (1895; *Acipenser*), Grande and Bemis (1991; polyodontids), Findeis (1993; *Scaphirhynchus*), and Arratia et al. (2001; *Polyodon*). The postcranial axial skeleton of *A. brevirostrum* is typical for Acipenseriformes and is composed of an unconstricted notochord (i.e., centra are entirely absent) and the surrounding elements of the vertebrae (aspondylous vertebrae in the terminology of Arratia et al., 2001). The vertebral column may be divided into the anterior abdominal region (i.e., rib-rearing) and the posterior caudal region, although the distinction between the two is blurred, particularly in small individuals in which the basiventrals or ribs have yet to fully form. Within the abdominal region, several (up to five) vertebrae become incorporated into the occipital region of the skull and in effect are part of the braincase (Fig. 29). Within the caudal region, we distinguish the preural and ural regions (the vertebra containing the parhypural is the posteriormost preural vertebra; the ural region of the vertebral column is described in the section Caudal Fin and Supports).

Acipenser brevirostrum has about 55 preural vertebrae (approximately 25 abdominals), although no attempt was made to make precise counts for our series because many specimens were too incomplete because of damage during preparation of dry skeletal material. Every vertebra (Figs. 76–78) is composed of four paired elements: basidorsals, interdorsals, basiventrals, and interventrals. Vertebrae of the abdominal region also support paired ribs and a median

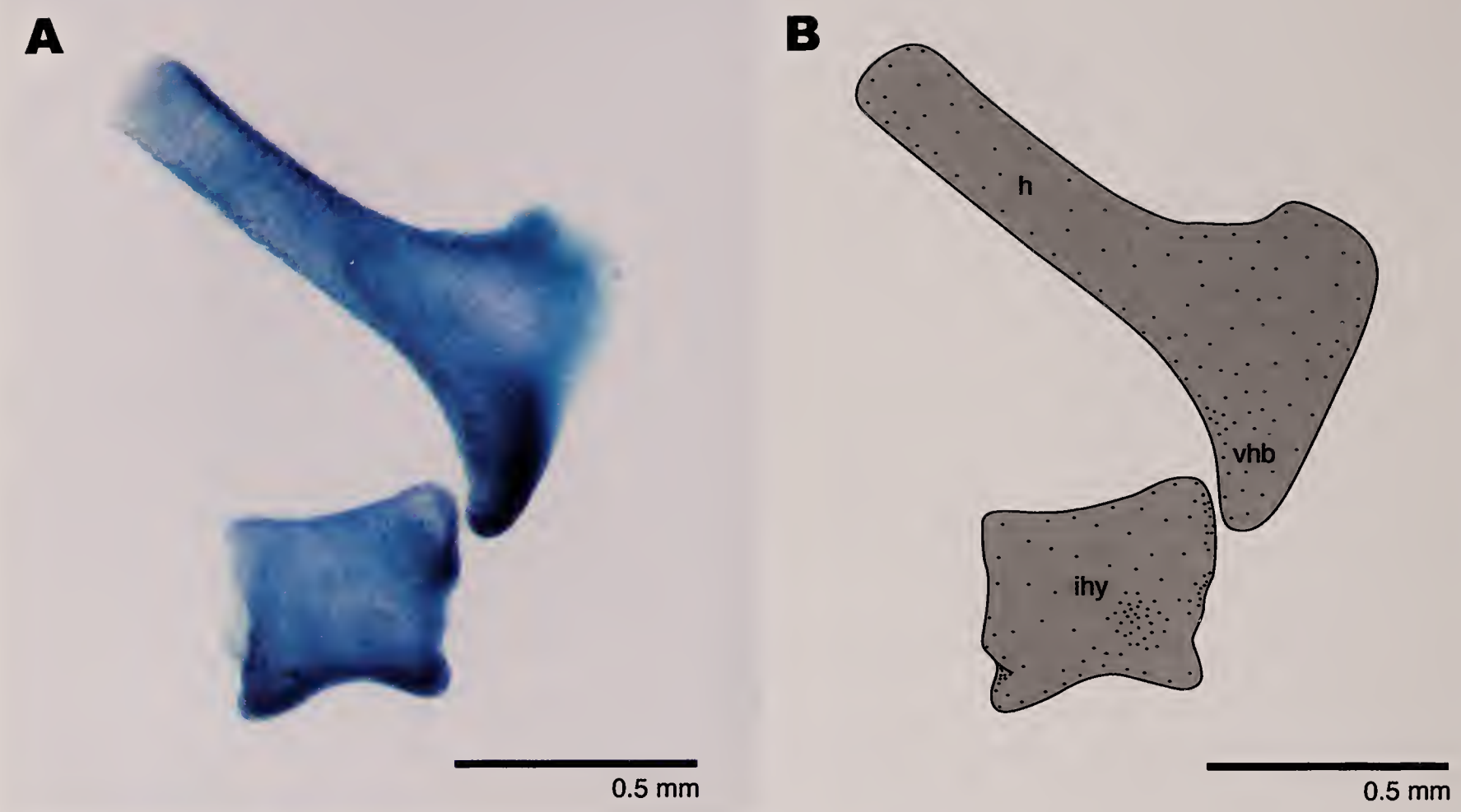


FIG. 66. *Acipenser brevirostrum*, dorsal portion of the hyoid arch at various stages of development, in medial view. (**A, B**) VIMS 12078, 23.3 mm TL. (**C, D**) VIMS 12086, 71 mm SL. Anterior to left. (**E, F**) VIMS 12087, 251 mm SL. Anterior to left. Abbreviations found on pages 8–9.

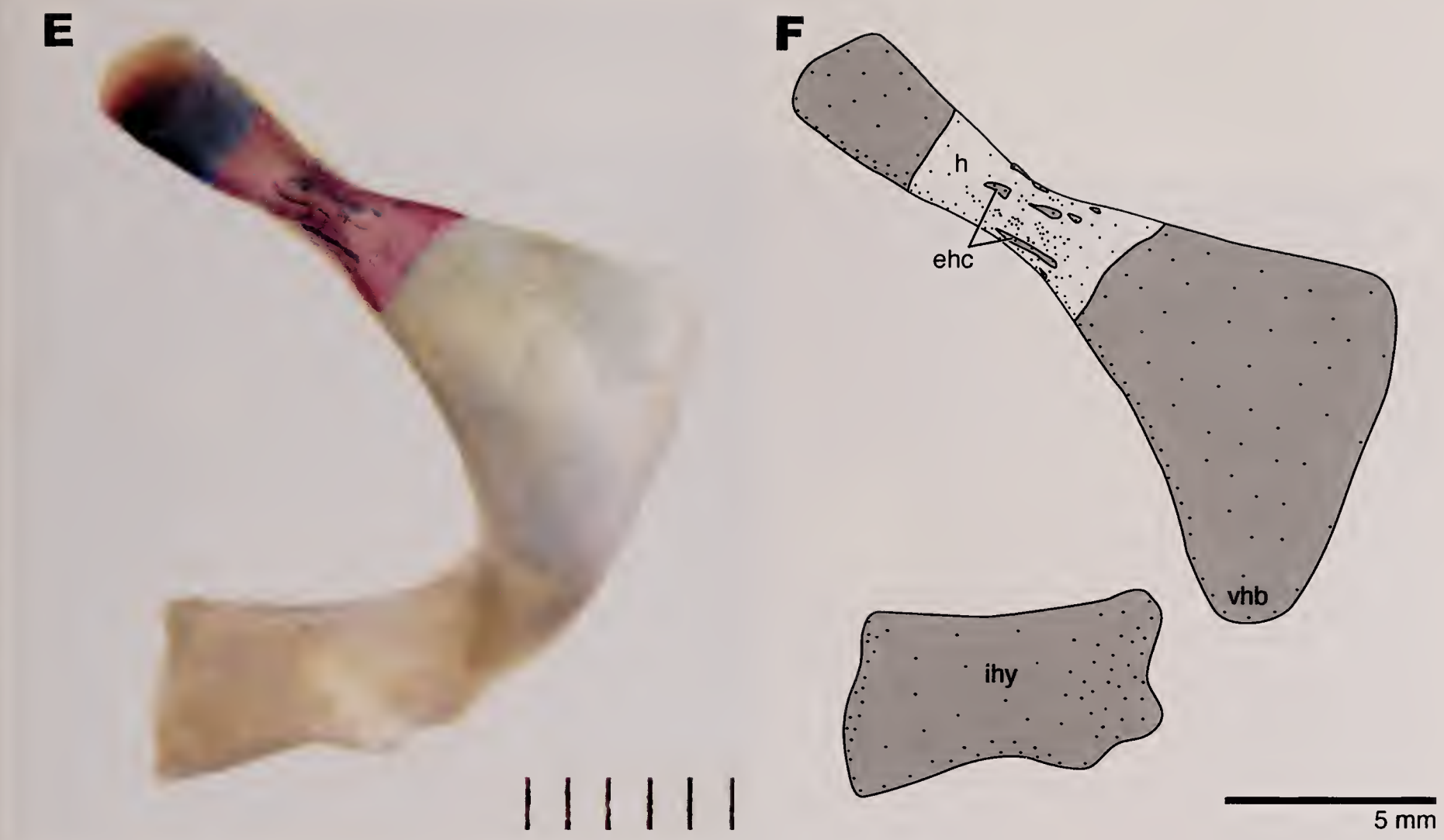


FIG. 66. *Continued.*

supraneural (vertebrae anterior to the dorsal fin); the posterior preural and ural regions also have a series of median supraneurals. All these elements, except for the interdorsals and interventrals, may ossify in adults, although the precise timing of their ossification is unclear. Not every vertebra has components of every series as a discrete element (i.e., fusions between adjacent elements are common).

The dorsalmost elements of the vertebrae of *A. brevirostrum* are the median supraneurals. In contrast to polyodontids, which possess a continuous series of supraneurals (although the elements below the dorsal fin are greatly reduced in size), the supraneural series of *A. brevirostrum* is interrupted, as in all members of Acipenseridae, so that there are predorsal supraneurals anterior to the dorsal fin and a posterior series of caudal supraneurals that lie dorsal to the ural neural arches (discussed in the section Caudal Fin and Supports). The anteriormost predorsal supraneurals associated with the occipital vertebrae are small elements, but these quickly grade posteriorly into more elongate bars of cartilage. For much of the abdominal region, these supraneurals are similar in size but then become gradually smaller in the series before disappearing entirely near the anterior base of the dorsal fin (Figs. 77, 78). In adults, all supraneurals are perichondrally ossified (Fig. 29). The supraneurals are the first vertebral elements to ossify. Arratia et al. (2001, p. 159) questioned the identification of these elements in Acipenseriformes as "true" supraneurals (i.e., a median element that develops independent of the neural arches, as found in most actinopterygians), citing their observations on small specimens of *Polyodon*, in which one or two of the anteriormost supraneurals were found to be continuous with "its" basidorsal. They concluded that separation of the supraneural from the neural arch was a secondary ontogenetic event in Acipenseriformes. However, we only rarely found the supraneurals and basidorsals to be fused in specimens of any size, and when this was found, it typically occurred only on one side (e.g., see Figs. 77, 78). Further, among the smallest specimens in which the supraneurals were present (e.g., FMNH 112215, 50.9 mm TL), they clearly are separate from the basidorsals (Fig. 76). Given that fusions frequently occur between adjacent vertebral cartilages in acipenseriforms (e.g., basidorsal–interdorsal fusions) and our ontogenetic observations on these elements in particular, we regard this series as true supraneurals rather than detached neural spines.

The basidorsal cartilages (**bd**, Figs. 76–78) are ossified as the neural arches of the adult (**na**, Fig. 78). In an 18.8 mm TL specimen of *A. brevirostrum*, we found about 18 pairs of basidorsals. In this specimen, these elements are most fully developed anteriorly and grade posteriorly to small specks of cartilage (i.e., the series develops in an anterior-to-posterior direction). In adults, the left and right basidorsals (= neural arches) remain separate from one another. Although precise timing could not be determined, the ossification of each basidorsal appears to begin dorsally on the element, immediately lateral to the supradorsal ligament, and progresses ventrally until it is ossified lateral to the spinal cord itself. In the neural arches posterior to vertebra 15 in one exceptionally well-ossified specimen (UMA F10578), we found this ventral portion to be separate from the main ossification of the neural arch, but because it was only a single instance, it is unclear how to interpret these bones (also, these posterior ventral ossifications were typically small and irregularly formed, suggesting that they are "different" from true neural arches). Arratia et al.

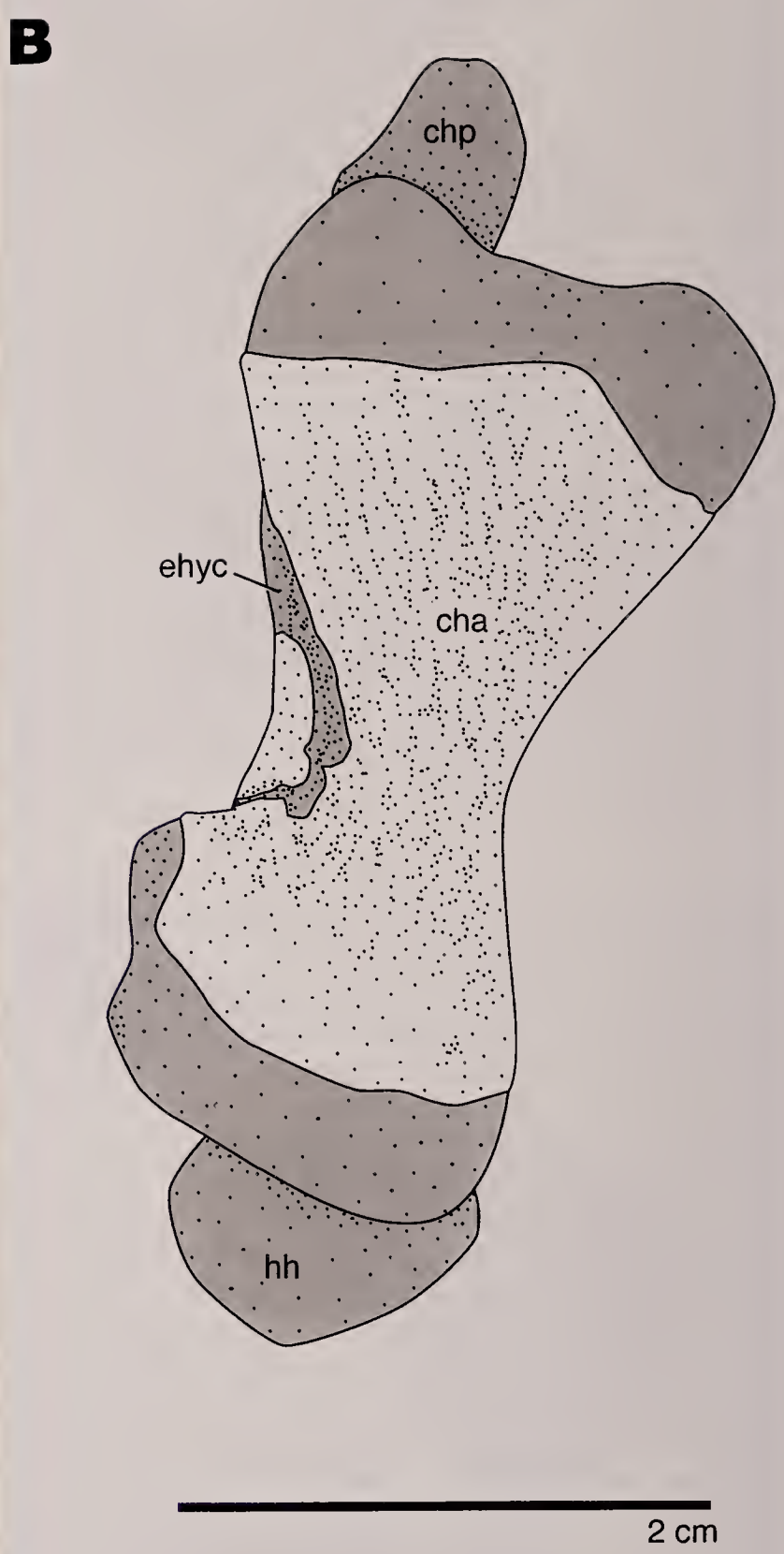


FIG. 67. *Acipenser brevirostrum*, ventral portion of the hyoid arch in ventral view, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing. In photo, bone is stained red, and cartilage appears white; in drawing, bone is white, and cartilage is gray. Anterior to left. Abbreviations found on pages 8–9.

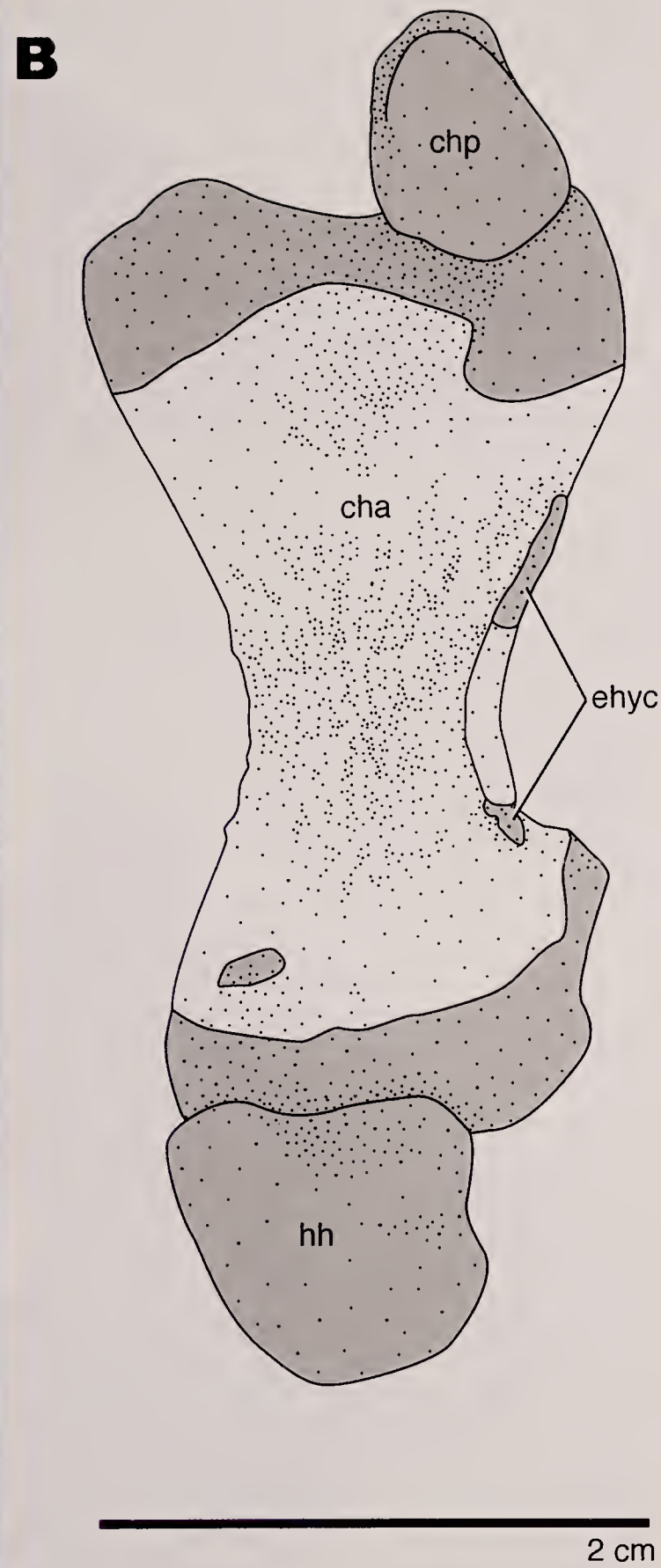


FIG. 68. *Acipenser brevirostrum*, ventral portion of the hyoid arch in dorsal view, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing. In photo, bone is stained red, and cartilage appears white; in drawing, bone is white, and cartilage is gray. Anterior to left. Abbreviations found on pages 8–9.

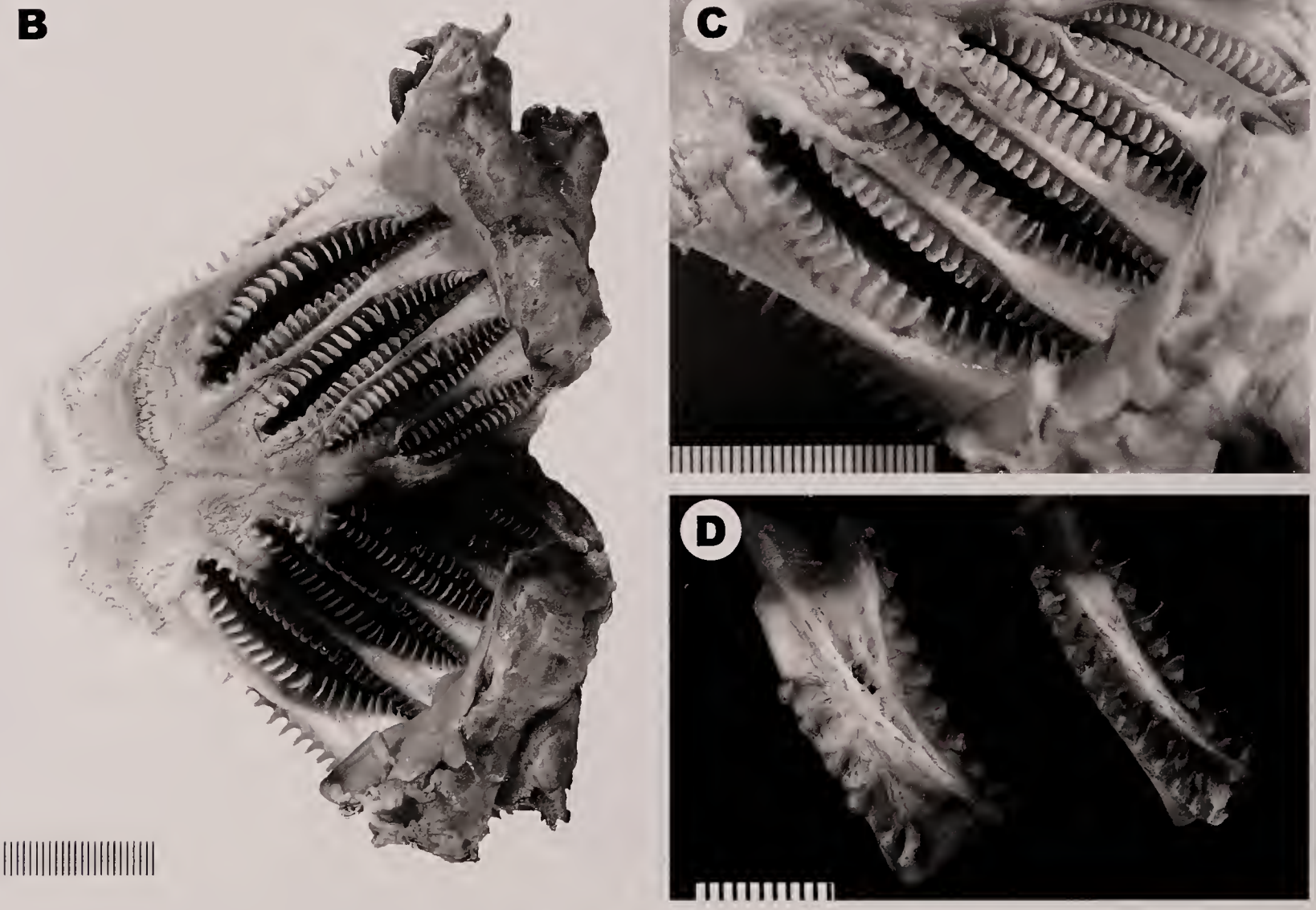


FIG. 69. *Acipenser brevirostrum*, branchial arches, from VIMS 12072 (female, 940 mm SL) prior to preparation as a dry skeleton. (**A**) Head in lateral view with opercular series dissected away to expose branchial arches, suspensorium and other mouthparts *in situ*. (**B**) Branchial arches in isolation in dorsal view (dorsal elements slightly displaced laterally) to show texture of skin in hypobranchial and basibranchial regions. (**C**) Close-up of intact left ventral elements to show form of gill rakers. (**D**) Dried skeletal preparations of left ceratobranchials 1 and 2 in dorsal view to show relationship of skeletal portion of gill rakers to the ceratobranchials. Scale in millimeters. Anterior to left in all.

FIG. 70. *Acipenser brevirostrum*, close-up of cleared and stained gill arches showing detail of developing gill rakers, from VIMS 12087 (251 mm SL). Portions of left ceratobranchials 1–3 shown in dorsal view (see Fig. 73B for orientation). Scale = 2 mm. Anterior to left.

(2001) consider the typical dorsal ossifications of the basidorsals to be neural spines in Acipenseriformes because of their dorsal position on the basidorsal. It is true that they are positioned dorsal to the spinal cord, as are the neural spines of more derived actinopterygians (e.g., neopterygians), which form as dorsal outgrowths of the neural arches (Arratia et al., 2001). This would mean, however, that the neural arches in sturgeons are outgrowths of the neural spine rather than vice versa or, alternatively, that the neural arches are lost entirely and that the ossification represents only the neural spine portion. Thus, regardless of the interpretation of these elements, the condition in sturgeons—and Acipenseriformes generally—is unusual (if not unique) among actinopterygians, and their homology with the bones found associated with the basidorsals of other fishes is unclear.

The interdorsals (**id**, Figs. 76–78) are small, roughly triangular cartilages positioned posteroventrally to the basidorsal that may become fused to the basidorsal cartilage. In the caudal region, there may be two interdorsals: a larger anterior element (**ida**, Figs. 77, 78) and a smaller, ovoid posterior element (**idp**, Figs. 77, 78).

In contrast to the basidorsals, the basiventrals (**bv**, Figs. 76–78) develop in a posterior-to-anterior direction (Fig. 75). In our smallest specimens, paired basiventrals are positioned along the notochord between the levels of the pelvic and anal fins. The same 18.8 mm TL specimen referred to in the description of the basidorsals (above) has 19 preural basiventral elements; these are most fully developed posteriorly in the caudal region, and the anteriormost elements are tiny nodules of cartilage. In adults, the basiventrals of the abdominal region are much larger than those of the caudal region and are deeply concave ventrolaterally, where they curve laterally to form pronounced parapophyses that articulate with the ribs. The parapophyses are broad and dorsally flattened anteriorly in the abdominal region and support a circular perichondral bone that, in adults, spreads medially to cover the main body of the basiventral; this bone ranges from a small circle of perichondral bone on the dorsal and ventral surface of the parapophysis to a collar of bone surrounding the entire cartilage. In the occipital vertebrae, the posterior extension of the parasphenoid separates the parapophyses from the rest of the vertebra (Figs. 29, 41). These occipital parapophyses differ from more posterior ones in that the articulation surface for the rib is a short, more or less rounded column of cartilage rather than a flattened bar-like element, and they are directed more ventrally than laterally.

The interventrals (**iv**, Figs. 77, 78) are similar to the interdorsals in shape (roughly triangular). They are positioned anterodorsally to the basiventral and may become fused to the basiventral. There is only a single pair of interventrals in each vertebra along the entire vertebral column (cf. interventrals of the caudal region; Figs. 77, 78).

We found as many as 27 pairs of ribs (**r**, Figs. 10, 29, 41, 76) in *A. brevirostrum*; it is possible that adults may have more than this number because ribs are easily lost during preparation. The ribs broadly contact the distal ends of the parapophyses. In adults, the ribs ossify as perichondral rods of bone around a cartilaginous core. Both the proximal and the distal tips of the ribs remain exposed as cartilage (i.e., the ossification of the rib does not extend to either tip); the length of the exposed cartilage is much greater distally than proximally. The first two ribs are flattened in adults to form bar-like rather than rod-like structures, and their distal tips are flattened and flared. The third and fourth ribs also are expanded distally. The ribs become more slender posteriorly. Dissection of several large specimens (e.g., FMNH 112913) revealed ribs positioned anterior to the first rib articulated with a basiventral. These floating ribs never contact the axial skeleton and are of varying size and shape, ranging from well-formed elements that "fit" into series with the more posterior ribs to irregularly shaped flattened bars. We are unsure of how common these floating ribs are because they are so easily lost during preparation of adult skeletons.

Caudal Fin and Supports

The caudal skeleton of sturgeons has been described and illustrated in many studies (e.g., Smith, 1956; Bartsch, 1988; Hilton, 2004; among others). The caudal fin of sturgeons generally is strongly heterocercal, with a dorsal lobe longer than the ventral lobe (Table 4) and distinctly forked (the ventral lobe of the caudal fin is subtle in juveniles of all sturgeon species and in adults *Scaphirhynchus* and *Pseudoscaphirhynchus*). The dorsal edge of the caudal fin of *A. brevirostrum* and of most basal actinopterygians is lined with a series of dorsal caudal fulcra (Table 5). These fulcra in sturgeons have always been interpreted as basal fulcra (*sensu* Patterson, 1982, as modified by Grande & Bemis, 1998, p. 25) because they are median structures. However, posteriorly, these single elements blend into a series of paired elements, that is, fringing fulcra (Fig. 83). The only other occurrences of fringing fulcra among extant actinopterygians are in lepisosteids and some megalopids (Forey, 1973; Patterson, 1982). In *A. brevirostrum*, there are up to 29 fulcra (basal and fringing) in this series (e.g., UMA F10579). Arratia (2009, p. 226) described this condition as her "Pattern II" basal fulcra, in which "the series of basal fulcra is formed anteriorly by unpaired elements that are forked proximally until the notch becomes so deep that the two halves become separate and the last elements of the series are all paired" (see Hilton, 2004, fig. 5, for illustration of both anterior and posterior dorsal caudal fulcra from *A. brevirostrum*). There is a single ventral caudal fulcrum in *A. brevirostrum*, as in other Acipenseriformes (e.g., †Chondrosteidae, Hilton & Forey, 2009; Polyodontidae, Grande & Bemis, 1991; see also Hilton, 2004); this is the first dermal element of the caudal skeleton to

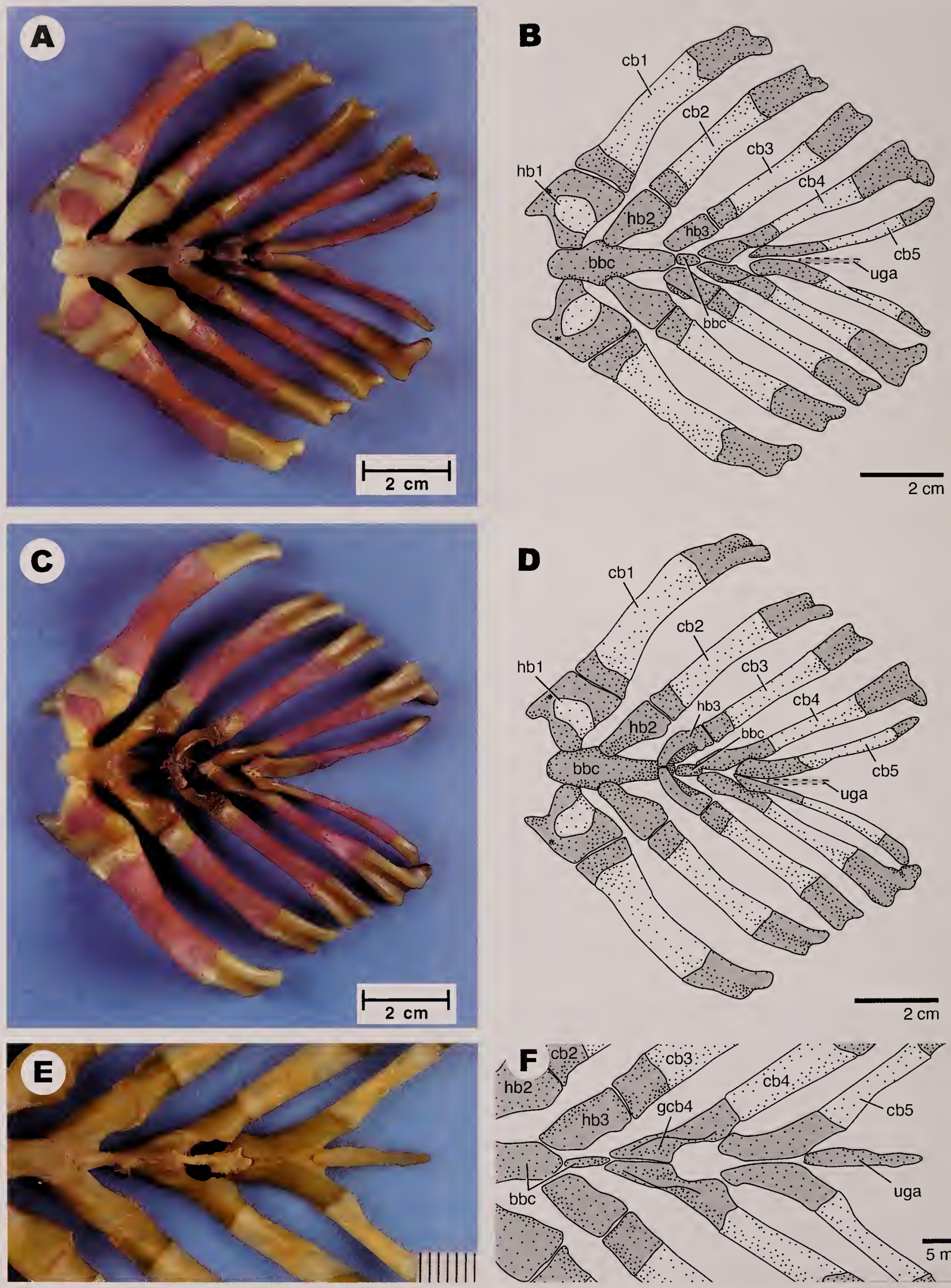


FIG. 71. *Acipenser brevirostrum*, ventral portion of the branchial arches. (**A**) Photograph and (**B**) line drawing of elements in dorsal view, from FMNH 113538 (female, 960 mm SL). (**C**) Photograph and (**D**) line drawing of elements in ventral view, from FMNH 113538 (female, 960 mm SL). In photos, bone is stained red, and cartilage appears white; in drawings, bone is white, and cartilage is gray. (**E**) Photograph and (**F**) line drawing of posterior portion of ventral gill arches in dorsal view showing typical arrangement (i.e., presence of posterior basibranchial element), from FMNH 112210 (female, 805 mm SL). Anterior to left. Abbreviations found on pages 8–9.

mineralize. Also associated with the caudal fin is a lateral field of overlapping rhomboidal scales on either side of the axial lobe of the caudal fin. These are described below in the section Scales.

The parhypural and hypurals are among the first elements of the postcranial axial skeleton to develop. In an 18.8 mm TL specimen, the posterior haemal arches and spines (including the parhypural) and the anterior hypurals were strongly developed (there are rudimentary basidorsal cartilages present in this specimen as well). These elements develop anteriorly and posteriorly from a central point (the precise point could not be determined from our specimens, but based on the distribution and sizes of the elements in our smallest specimens, it must be near or just posterior to the preural–ural boundary). The hypural series reaches the posterior tip of the notochord by 20.5 mm TL, although the posteriormost hypural elements are no more than tiny nodules of cartilage. Posteriorly these hypural elements become irregular, and adjacent elements fuse together (Fig. 82).

In the specimen illustrated in Figure 83, we found eight distal caudal radials (not illustrated), none of which were ossified. This is significant because many elements typically not ossified were ossified in this specimen, strongly suggesting that the distal caudal radials never ossify. These were associated with the haemal spines of preurals 1–3 and hypurals 1–5. Other specimens (e.g., Figs. 81, 82) have fewer distal caudal radials associated with preurals 1–3 and hypural 1.

The caudal supraneurals develop as a series prior to the stage in which the basidorsals (neural arches) reach into the ural caudal region. The supraneurals are well developed by 42.3 mm TL and are typically the only dorsal series of elements in the ural region to ossify (e.g., Fig. 82), although the basidorsals may also ossify as neural arches in the caudal region of large specimens (Fig. 83). Anteriorly in the series, it appears that several adjacent elements fuse together prior to ossification, as a single, elongate anterior supraneural is associated with several basidorsals (Fig. 82), whereas prior to ossification, a supraneural is matched to each basidorsal (Fig. 81). Posteriorly in the ural region, the supraneurals and basidorsals are indistinguishable, and adjacent elements become fused to form an irregular but continuous cartilaginous structure that may also contact or become continuous with the posterior hypural series at the posterior tip of the tail (e.g., Figs. 80–82). Arratia et al. (2001, p. 149) questioned the identification of these elements as supraneurals (e.g., Grande & Bemis, 1991), stating that "the origin and role of these elements in the caudal region [in Acipenseriformes] do not correspond to the origin and role of supraneurals in other actinopterygians. By comparison to other fishes these elements may correspond to the neural spine plus the supraneural or the neural spine plus the radial." We continue to refer to this as a series of supraneurals because they develop as independent, median cartilages that are positioned dorsal to the basidorsals (Fig. 80). An alternative hypothesis is that this is a series of epural elements (G. Arratia, pers. comm.). Although there may be some serial correspondence between supraneurals and epurals (i.e., epurals are recognized as a distinct series only because of the phylogenetic loss of subdorsal supraneurals; Patterson, 1973; Grande & Bemis, 1991, 1998; for differing interpretations, see Schultze & Arratia, 1989; Arratia et al., 2001), we do not favor terming these elements "epurals" in acipenserids because in a relatively closely related taxon (Polyodontidae) and more basal taxa (e.g., Polypteridae), the series in the caudal region is continuous with more anterior supraneural series. This condition is therefore considered to be plesiomorphic for Actinopterygii, and the "interrupted" series in Acipenseridae is best interpreted as homoplastic with the condition found, for instance, in Neopterygii (see also discussion by Grande & Bemis, 1991, p. 114). We do concur with Arratia et al. (2001, p. 149), however, that these elements in Acipenseriformes, "whatever the correct interpretation, [the form of these elements] is an unusual condition among actinopterygians and sarcopterygians."

Dorsal and Anal Fins and Supports

The dorsal fin is positioned between the levels of the pelvic fins and the anal fin (Table 1) and has a significantly longer base than the anal fin (Table 4). The dorsal and anal fins and their supports in *A. brevirostrum* (Figs. 84, 85, and 86, 87, respectively; Table 6) are composed of similar series of elements. Supporting each fin are the pterygiophores (we use "pterygiophore" to refer collectively to a series of proximal, middle, and distal radials; in general, these lie in series with one another). Both the proximal and the middle radials are simple rod-like elements, whereas the distal radials are smaller and more irregular in their shape; the distal radials are never known to ossify, whereas the middle and distal radials become surrounded by perichondral bone. There is much individual variation in the number and fusion patterns of elements of all series, particularly the proximal and middle elements (i.e., a single proximal element with more than one distal tip lies in series with multiple elements of the middle and distal series). The middle radial series of both fins is the first to develop (present in 18.8 mm TL specimens), followed by the proximal and finally by the distal radial series (Figs. 79–81); distal radials were first observed in 42.3 mm TL specimens. The fin rays of both median fins are more numerous than the series of radial elements that support them, a pattern found in all nonneopterygian actinopterygians. A single scute-like basal fulcrum is present at the anterior base of the dorsal and anal fin (**dbf**, Fig. 84, and **abf**, Fig. 86, respectively); there are no fringing fulcra on either fin.

Pectoral Fin and Girdle

The dermal component of the pectoral girdle of sturgeons is formed by five paired bones (posttemporal, supracleithrum, cleithrum, postcleithrum, and clavicle) and a median interclavicle. The chondral component of the girdle is comprised of the suprascapular cartilage and the scapulocoracoid cartilage and its ossifications (scapula, coracoid, and mesocoracoid). The posttemporal is incorporated into the skull roof and is described and illustrated in the section Bones of the Skull Roof and Circumorbital Region. The pectoral girdle and fin of *Acipenser*, including the musculature, nerves, and blood supply, were described in detail by Jessen (1972) based on *A. sturio*. The early development of the pectoral fin supports of *Acipenser* was described by Davis et al. (2004) based on *A. transmontanus*.

The supracleithrum (**scl**, Figs. 8, 15, 16, 18, 26, 35–37, 88–92) is a tall, heavily ossified bone. Its ornamented superficial component is roughly triangular in shape, although the anterior margin is slightly concave. A large, unornamented dorsal component forms a broad lap suture with the

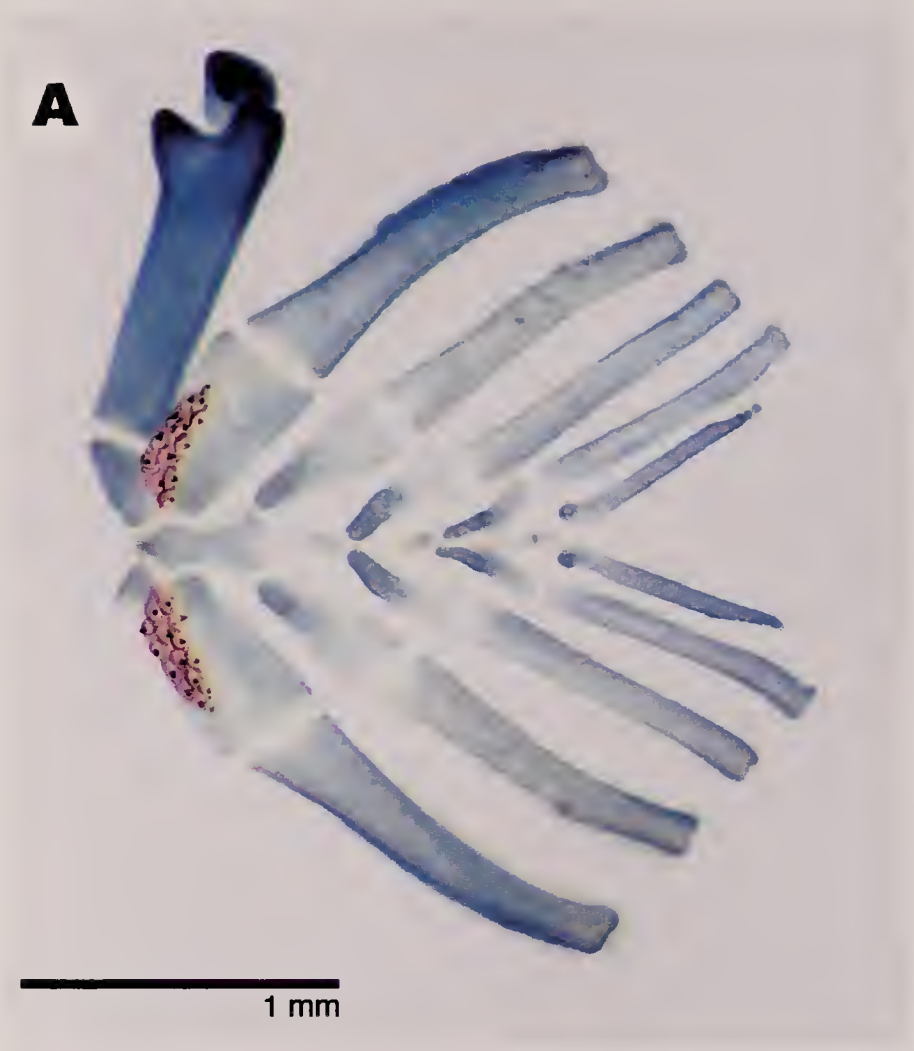


FIG. 72. *Acipenser brevirostrum*, ventral portion of the gill arches at various stages of development, in dorsal view. (**A, B**) VIMS 12078, 23.3 mm TL. (**C, D**) FMNH 112916, 85.5 mm SL. Anterior to left (**E, F**) VIMS 12087, 251 mm SL. Anterior to left. Abbreviations found on pages 8–9.

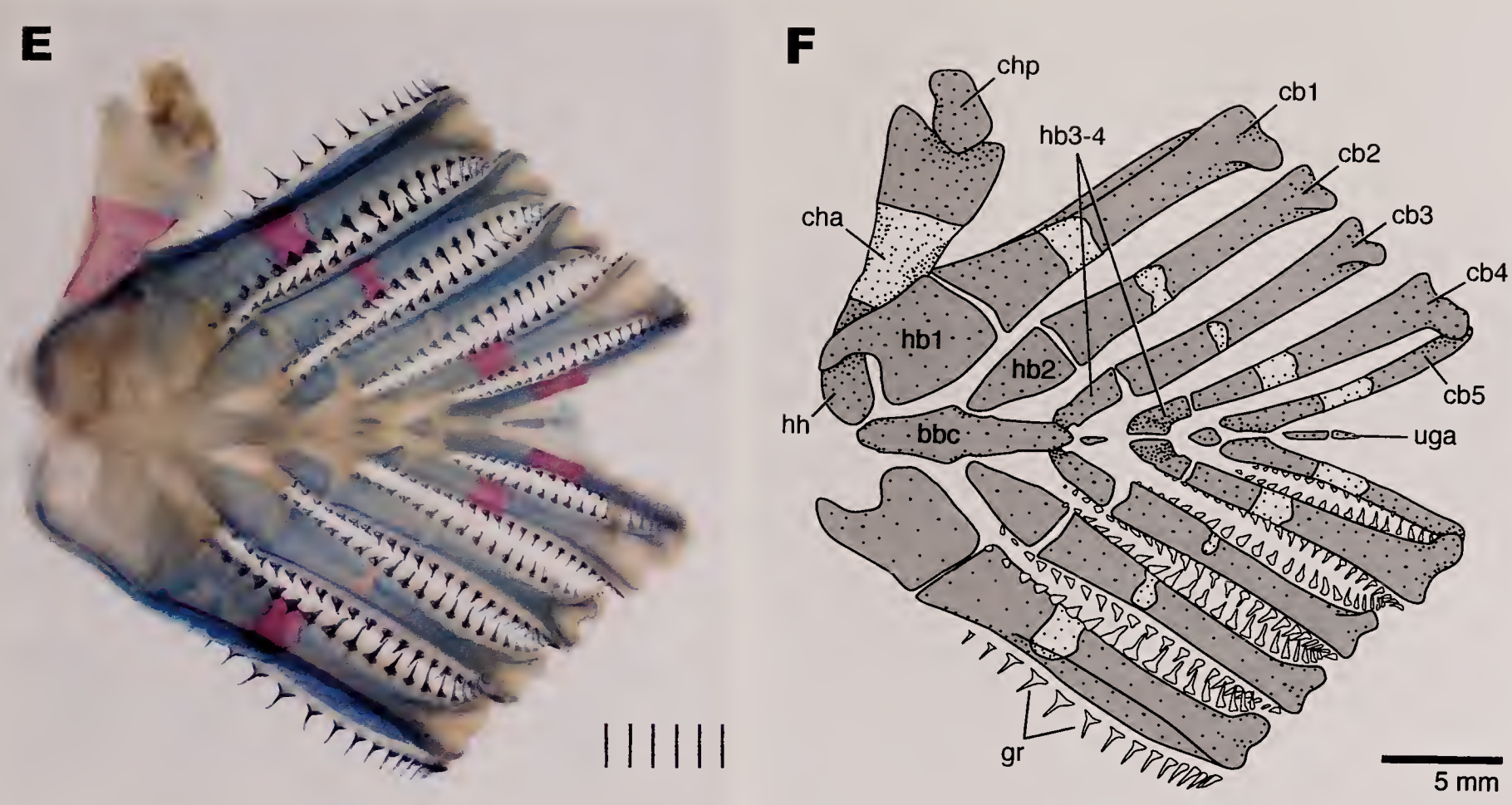


FIG. 72. *Continued.*

posterolateral corner of the posttemporal. Ventrally, the supracleithrum broadly overlaps the dorsolateral portion of the cleithrum.

The cleithrum (**cl**, Figs. 15, 16, 26, 35–38, 88–94) of *A. brevirostrum* resembles that of other sturgeons. Its distinct dorsal process partially contacts the supracleithrum. This process bears lateral and medial ridges and is continuous with ventral ornamented portion of the cleithrum. The anteroventral surface of the cleithrum is unornamented where it is overlapped by the clavicle. The margin of the cleithrum is irregularly shaped, although there is always a broad, overlapping suture with the clavicle. The other distinct portion of the cleithrum is an anteromedial membrane bone extension that forms a shallow depression that, together with a similar bony lamina from the clavicle (see below), forms the so-called opercular wall (Findeis, 1993, 1997).

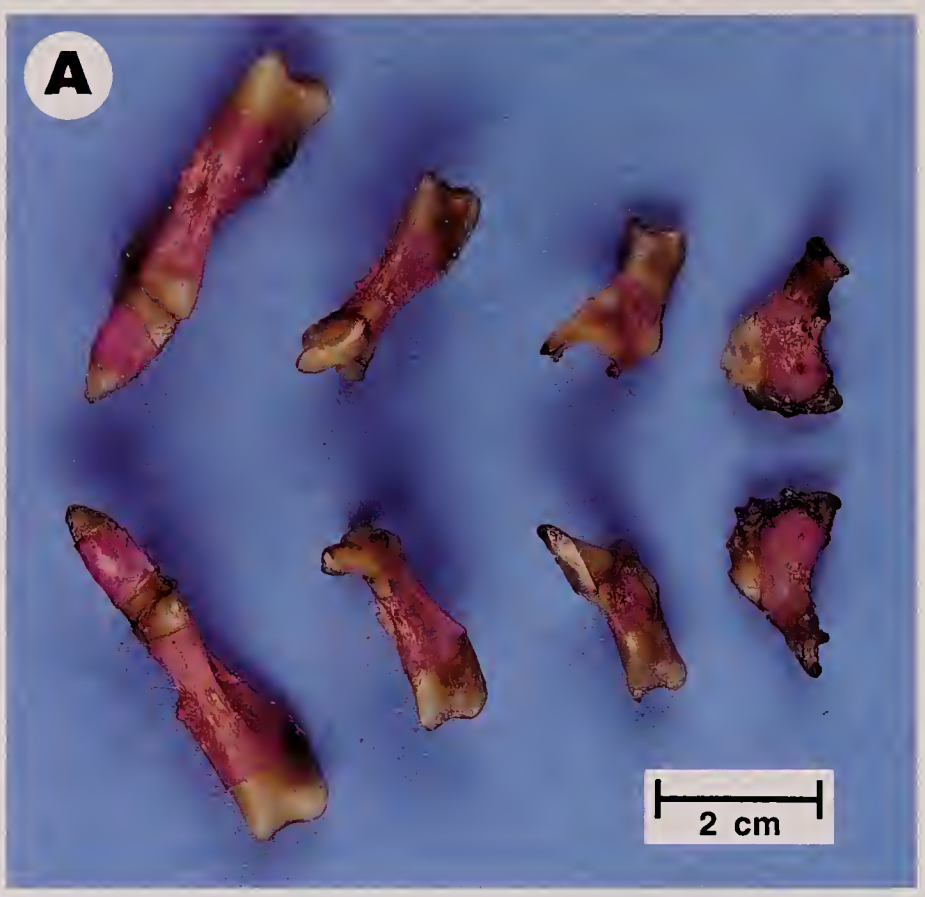
The slender, irregularly shaped postcleithrum (**pcl**, Figs. 8, 15, 16, 26, 35, 36, 88, 89, 91, 92) closely contacts the lateral surface of the scapulocoracoid cartilage. The postcleithrum lies posterior to the supracleithrum at the point where it overlaps the cleithrum. The lateral surface of the postcleithrum is variably ornamented and may be completely smooth and not visible externally. It was first found as a small splint of bone in our 24.8 mm TL specimen.

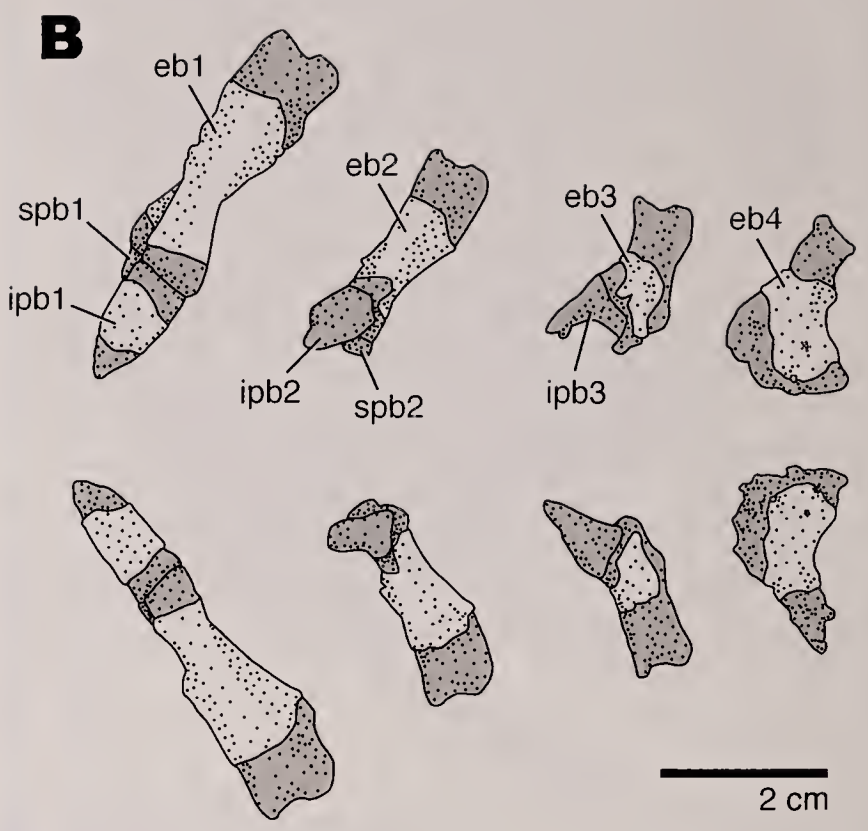
The clavicle (**clv**, Figs. 26, 35–38, 88–93) is the largest bone of the ventral portion of the dermal pectoral girdle. In ventral view (Fig. 38), it is a relatively broad, ornamented bone that posteriorly contacts the cleithrum to form the so-called cardiac shield (Findeis, 1997). Anteromedially, the left and right clavicles contact one another along the midline but do not form a tight suture. At its anteriormost extent, the clavicle bears a lateral extension that, while variable in its prominence, was found in all specimens of *A. brevirostrum*. The dorsal surface of the clavicle bears a large membrane bone lamina that overlaps the similar lamina of the cleithrum. These two laminae make up the opercular wall (Findeis, 1993, 1997), which defines the posterior limits of the branchial chamber. The dorsal and medial margins of the opercular wall are jagged and irregularly shaped, and the degree of ossification (i.e., the thickness of the bone) is individually variable (Hilton & Bemis, 1999, fig. 9). Both the cleithrum and the clavicle were found in a 20.5 mm TL specimen.

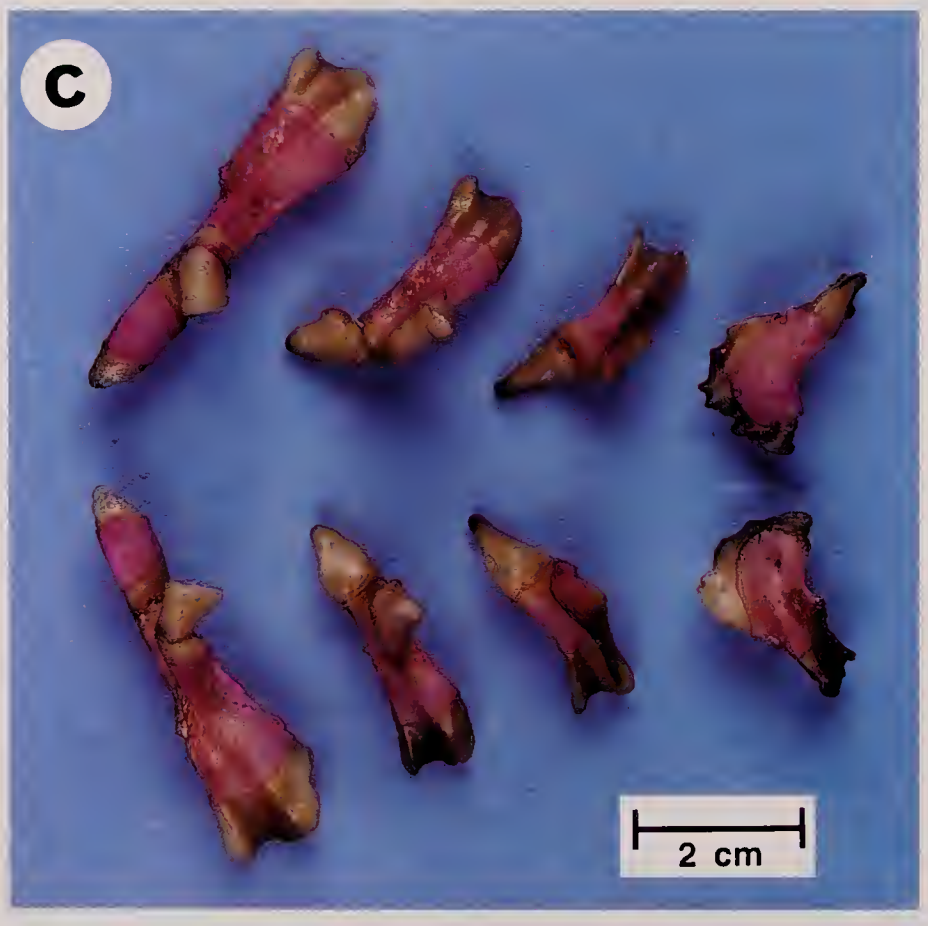
The most variably shaped bone of the dermal pectoral girdle in *A. brevirostrum* is the interclavicle (**iclv**, Figs. 38, 89, 91, 93). This is the only unpaired bone of the pectoral girdle and is positioned dorsal to the left and right clavicles at the point at which they meet in the midline. The smallest specimen to have an interclavicle was 27.6 mm TL. Because the interclavicle lies deep to the skin, it is unornamented, although it may extend posteriorly so that it is visible in ventral view in skeletal preparations.

The suprascapular cartilage (**sscc**, Fig. 90) is a laterally compressed splint of cartilage tightly associated with the medial surface of the supracleithrum, and positioned lateral to the dorsalmost portion of the cleithrum. It is broadest dorsally and tapers to a point ventrally. The suprascapular cartilage was never found to be ossified.

The scapulocoracoid cartilage (**scc**, Figs. 88, 90, 92, 93) of *A. brevirostrum* was illustrated by Findeis (1997, fig. 9; our terminology for some of its regions differs from that used by Findeis) and Hilton and Bemis (1999, fig. 9). This cartilage is a robust, complexly shaped element. Dorsal to the glenoid ridge (the middle region that forms the articulatory surfaces for the propterygium, radials, and metapterygium; Findeis, 1997), the scapulocoracoid forms an arch with a thick dorsal extension that contacts the medial surface of the supracleithrum and the posterior surface of the cleithrum (the dorsal process of the scapula of Jessen, 1972, fig. 2). Ventral to this is a lateral







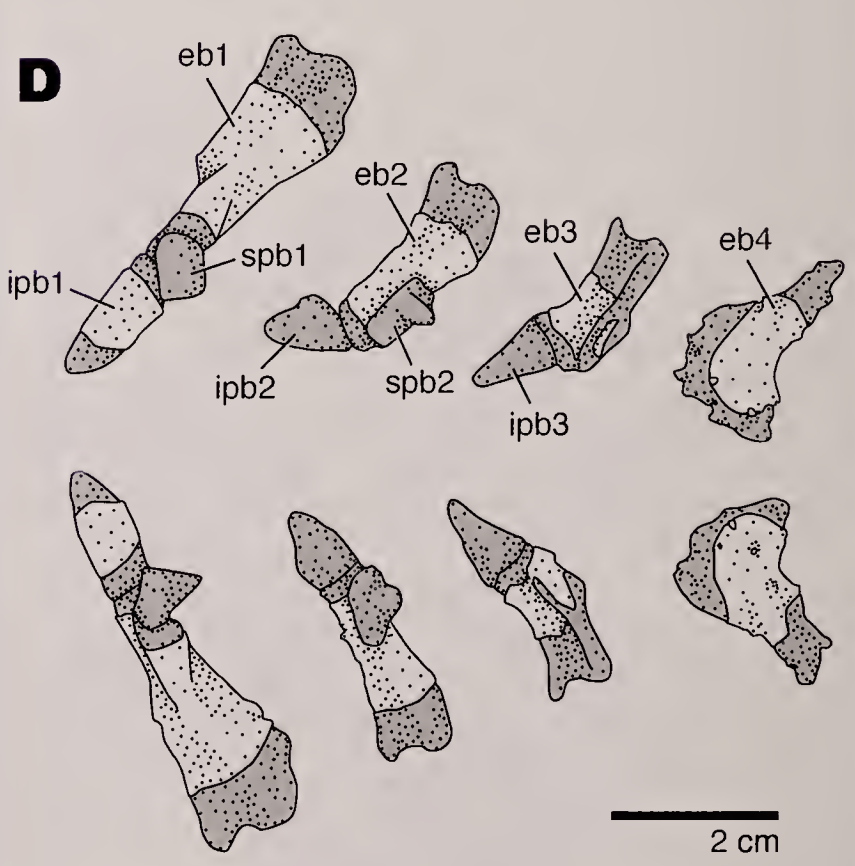


FIG. 73. *Acipenser brevirostrum*, dorsal portion of the branchial arches, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing of elements in ventral view. (**C**) Photograph and (**D**) line drawing of elements in dorsal view. In photos, bone is stained red, and cartilage appears white; in drawings, bone is white, and cartilage is gray. Anterior to left. Abbreviations found on pages 8–9.

mesocoracoid arch (Findeis, 1997) that lies against the medial surface of the posteroventral portion of the cleithrum. Dorsally, this arch is thin and is thickest ventrally where it joins the glenoid ridge and supports the articulation of the propterygium. Dorsal to the glenoid ridge is the median scapular arch (= the cleithral arch of Findeis, 1997). Together, the mesocoracoid and scapular arches define the roof and walls of a canal. At the level of the glenoid ridge, an anterior and lateral bridge of cartilage (the propterygial bridge of Findeis, 1997) contacts the medial surface of the cleithrum and serves as an attachment site for the pectoral adductor musculature (Jessen, 1972). The propterygial bridge extends anteriorly so that it spreads dorsally onto the medial surface of the clavicle. Ventral to the glenoid ridge, the scapulocoracoid continues in the same plane as the scapular arch until it contacts the dorsal surface of the clavicle, thereby forming the coracoid arch (= the coracoid wall of Findeis, 1997) of the scapulocoracoid. The coracoid arch forms the medial wall of the fossa for the pectoral abductor musculature (Jessen, 1972). The coracoid arch spreads out both laterally and predominantly anteriorly to form a thin sheet of cartilage, the coracoid shelf (Findeis, 1997), that lies flush against the dorsal surface of the clavicle.

Contrary to Jollie (1980), we found several ossification centers of the scapulocoracoid cartilage that we interpret as homologues of the scapula (ossifies in the scapular arch; **sc**, Figs. 88, 90, 92), the coracoid (ossifies in the coracoid arch; **cor**, Figs. 88, 90, 92), and the mesocoracoid (ossifies in the mesocoracoid arch; **mcor**, Fig. 92) of other actinopterygians. There is much variation in the extent of these ossifications—and even in their presence—between similarly sized specimens of similar estimated ages (Hilton & Bemis, 1999). For example, in one of the largest specimen of *A. brevirostrum* examined here (FMNH 113538, Figs. 88, 90, 92), we discovered an ossified mesocoracoid bone that is completely separate from the other ossifications of the scapulocoracoid. In other large specimens (e.g., >800 mm SL), the ossification of this portion of the scapulocoracoid cartilage is continuous with the bone of the scapular and coracoid arches (e.g., see Hilton & Bemis, 1999, fig. 9), and it is likely that three distinct centers of ossification are present.

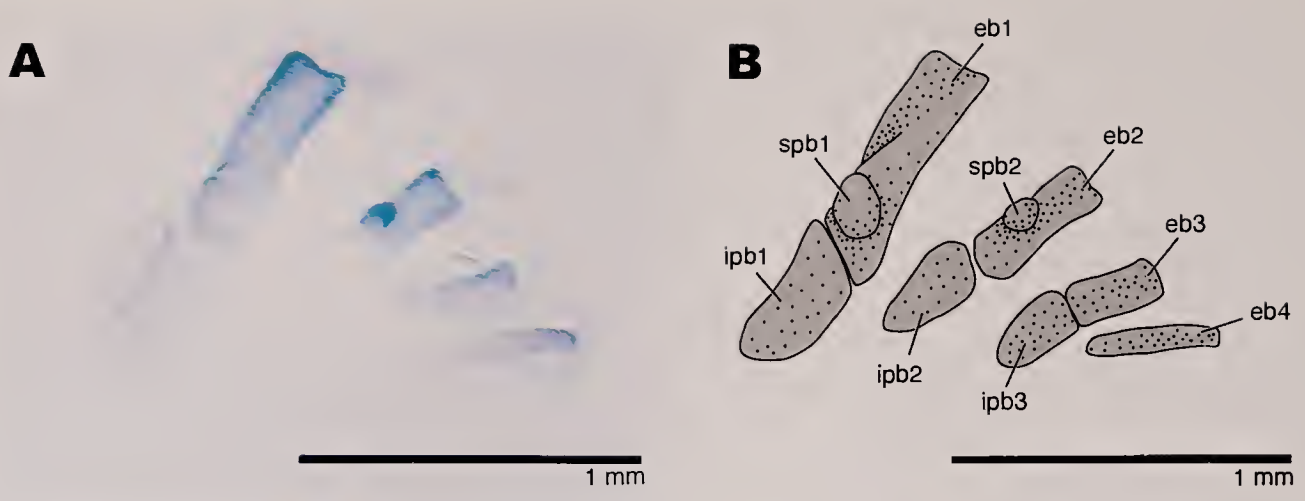
The skeletal support of each pectoral fin includes perichondrally ossified radials—propterygium and metapterygium—and cartilaginous distal radials. The propterygium (**ptg**, Figs. 90, 92, 93) ossifies relatively early in ontogeny and becomes intimately associated with the base of the pectoral fin spine (see below). A variable number (at least two or three) of proximal radials (**ra**, Figs. 88, 90, 92, 93) lie between the propterygium and metapterygium and articulate directly with the glenoid ridge of the scapulocoracoid (= mesopterygial radials of Davis et al., 2004). The broad metapterygium (**mtg**, Figs. 88, 90, 92, 93) is the medialmost supporting element for the pectoral fin rays to articulate with the scapulocoracoid. The metapterygium itself supports two or three radials (metapterygial radials of Davis et al., 2004), giving it a branching appearance. The distal radials (**dr**, Figs. 88, 90, 92, 93), which do not ossify, form the distalmost series of elements supporting the pectoral fin. These small, irregularly shaped elements were not observed in specimens smaller than 30.5 mm TL.

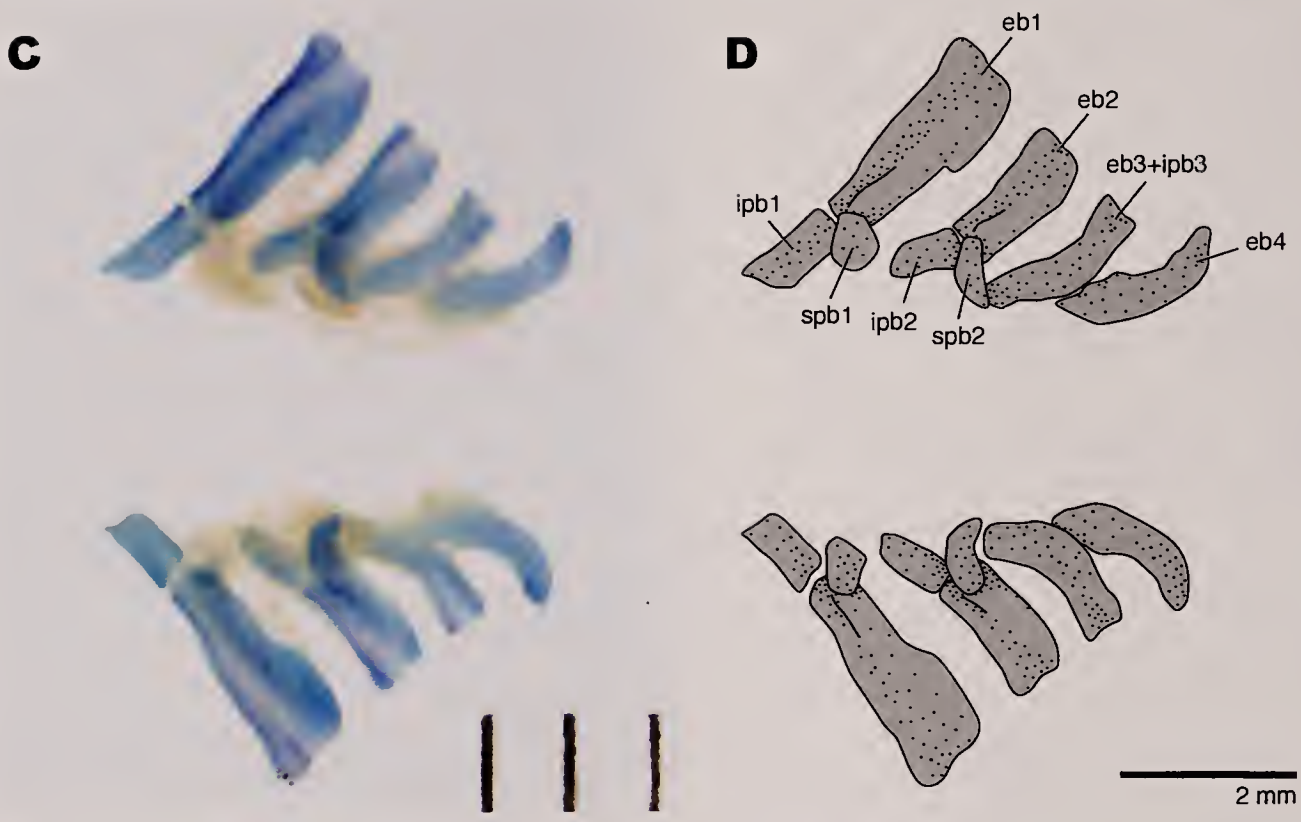
A striking feature of the pectoral fin is the stout spine that forms its leading edge (**pfs**, Figs. 7, 26, 38, 88–93). The pectoral fin spine forms early in ontogeny and is recognizable as a faint spine by 21.9 mm TL (Fig. 93A, B). In adults, the distal tip of the fin spine shows "typical" fin-ray–like anatomy (i.e., the free tip consists of a series of bony segments representing two or maybe three individual fin rays), but it is heavily ossified proximally and bears ridges or striations along much of its axis (Figs. 88–92). Findeis (1993) described and illustrated the development of the fin spine in acipenserids (see also Findeis, 1997, fig. 2) and determined that the spine was not formed by the mere fusion of adjacent fin rays but that additional dermal bone surrounds the bases of the fin rays along the leading edge of the fin (perhaps represented by the "faint spine" observed in our study). Findeis (1997) further suggested that the varying robustness of the fin spine, both between taxa and through ontogeny, is due to a variable number of fin rays that ultimately become incorporated into the fin spine. This may be the primary source of variation in the robustness of the spine across taxa but is likely not the only source of variation. The robustness of the spine likely also reflects the thickness of the ossification of the fin rays forming the spine, both individually and collectively. However, it will be important for future comparative studies to document the number of fin rays that are included in the spine across ontogeny and species of sturgeons.

Pelvic Fin and Girdle

Skeletal supports of the pelvic fins of sturgeons were illustrated and described by Mollier (1897), Sewertzoff (1926a, 1934), and Findeis (1993), among others. The pelvic fin of *A. brevirostrum*—and acipenserids generally—is supported by the basipterygium (formed of fused basipterygial or proximal radial elements, Sewertzoff, 1926a; **be**, Figs. 95, 96; see below) and a series of middle and distal radials; only the basipterygial elements (as the pelvic bone; **pb**, Fig. 95) and the middle radials ossify in *A. brevirostrum*. Sewertzoff (1926a) described a series of elements proximal to the proximal radials (his *basalia proximalia*) in early stages of development in *A. ruthenus*, although we could not find these elements in our study of *A. brevirostrum*, and they have not been reported by anyone else.

The paired basipterygia are composed of cartilaginous plates formed by the fusion of proximal (basipterygial) radials. Sewertzoff (1926a) termed this structure the *basale commune* and the free elements radials (in 1934, however, he referred to these as the basipterygium and metapterygia). Grande and Bemis (1991) considered the whole complex to be formed of basipterygial elements in polyodontids; the free elements were termed accessory basipterygia by Findeis (1993). Even in adult *A. brevirostrum*, some of the posterior proximal radials remain autogenous. The basipterygium in adults curves ventrally and bears a hooked process on its dorsal surface (**dpp**, Fig. 95) that serves as an attachment site for anterior pelvic musculature. Dorsolaterally, the basipterygium is deeply embedded in adipose tissue. A pelvic bone (i.e., the perichondral ossification of the basipterygium) was found in large specimens of *A. brevirostrum* (UMA F10431, UMA F10578, and FMNH 113538). These ossifications are present in specimens at least 899 mm SL; a more precise length at first ossification is impossible to determine with our dermestid-prepared skeletons, as these elements are easily lost during preparation (e.g., lightly ossified elements may be consumed by beetles). These elements are much





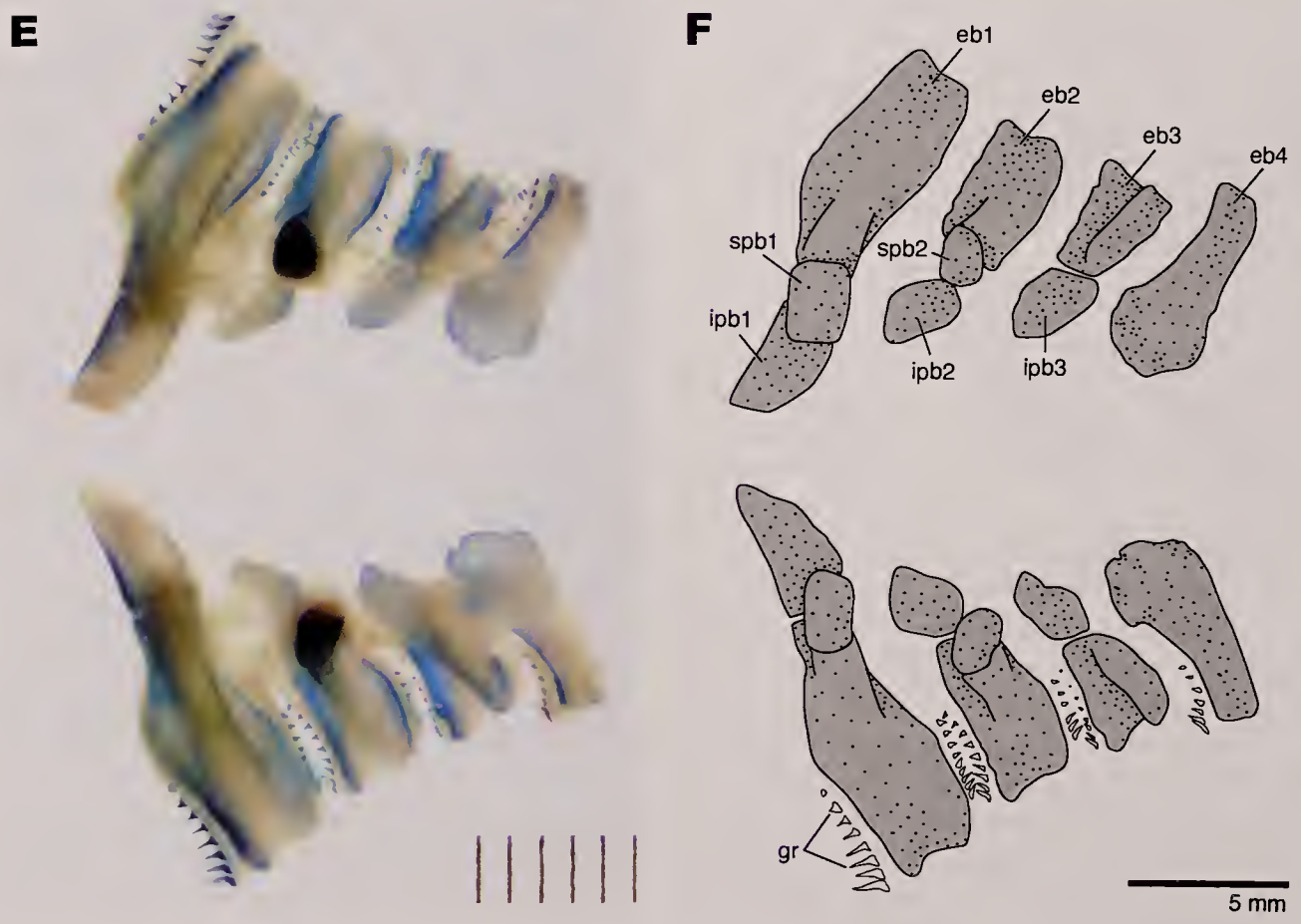


FIG. 74. *Acipenser brevirostrum*, dorsal portion of the gill arches at various stages of development, in dorsal view. **(A, B)** VIMS 12078, 23.3 mm TL (the left side of this specimen was damaged during dissection, so only the right side is illustrated). **(C, D)** FMNH 112916, 85.5 mm SL. Anterior to left. *Acipenser brevirostrum*, dorsal portion of the gill arches at various stages of development, in dorsal view, continued. **(E, F)** VIMS 12087, 251 mm SL. Anterior to left. Abbreviations found on pages 8–9.

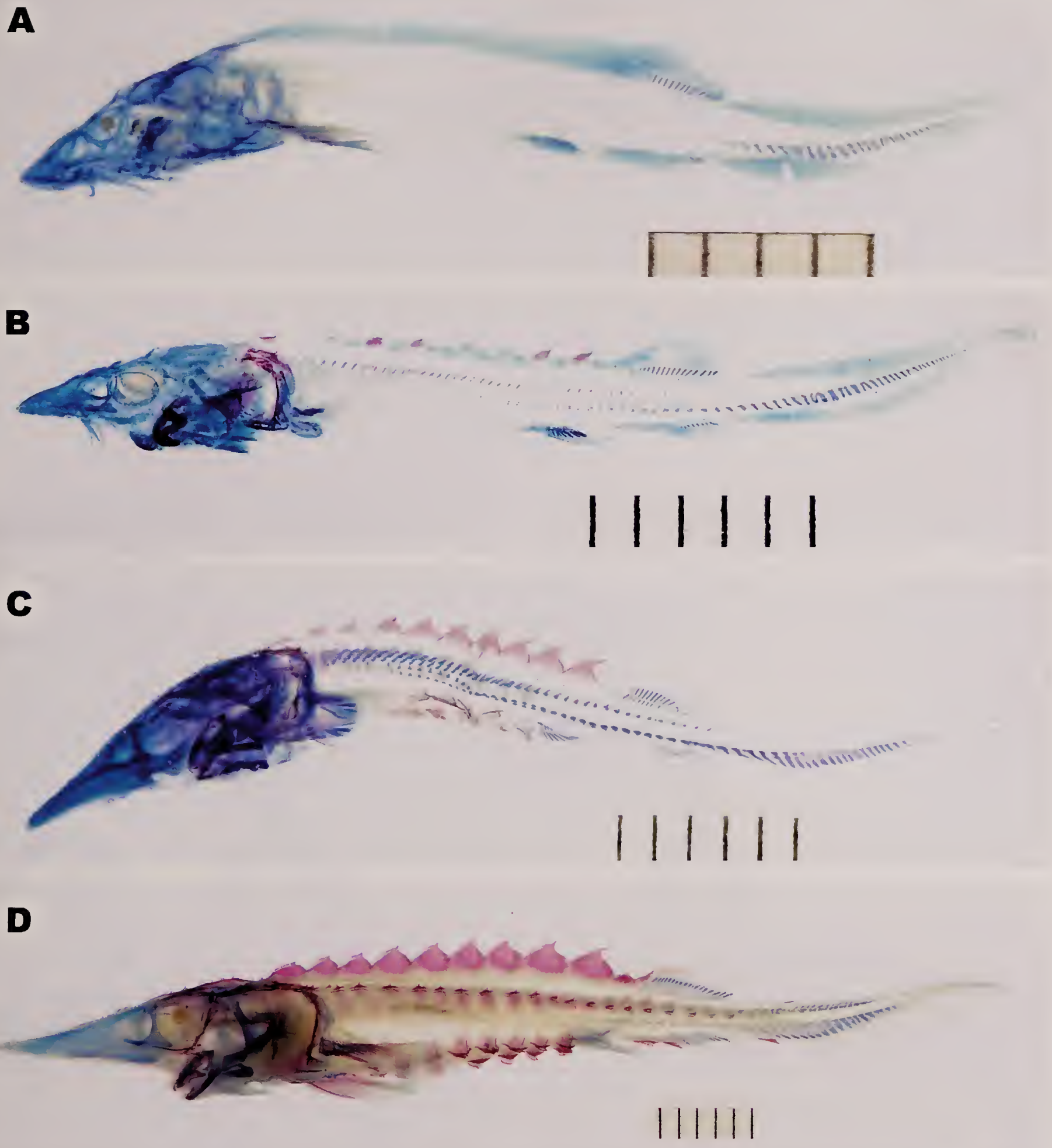


FIG. 75. *Acipenser brevirostrum*, growth series of cleared and stained specimens. (**A**) VIMS 12075, 19.8 mm TL. (**B**) VIMS 12077, 21.9 mm TL. (**C**) VIMS 12088, 30.5 mm TL. (**D**) VIMS 12082, 58.5 mm TL. Scale in millimeters. Anterior to left.

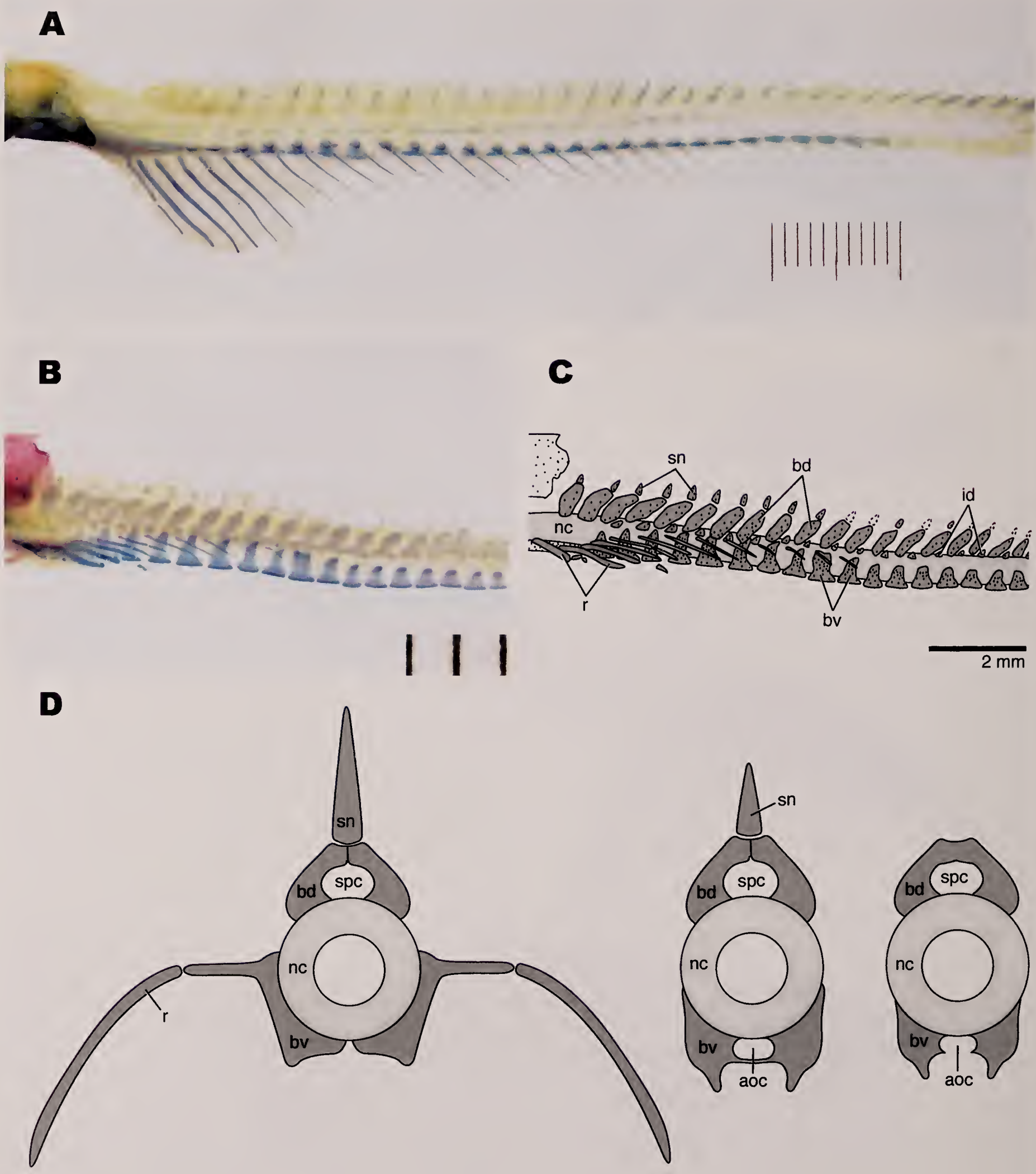


FIG. 76. *Acipenser brevirostrum*, vertebrae. (**A**) Abdominal vertebrae from a cleared and stained individual (VIMS 12102, 166 mm SL). (**B**) Anterior portion of abdominal vertebrae (FMNH 112215, 50.9 mm SL) showing ribs developed on anterior abdominal vertebrae only. (**C**) Line drawing of **B**. (**D**) Schematic cross sections of (left to right) an abdominal vertebra, a caudal vertebra anterior to dorsal fin, and a caudal vertebra posterior to dorsal fin. Scale in millimeters. Anterior to left in **A–C**. Abbreviations found on pages 8–9.

smaller than are the comparable bones found in *Scaphirhynchus* (Findeis, 1993, fig. 42) and *Polyodon* (Grande & Bemis, 1991, fig. 22).

The middle radials (= proximal radials of Sewertzoff, 1926a; **prm**, Figs. 95, 96) of the pelvic fin are elongate rod-like elements that ossify perichondrally relatively late in ontogeny (e.g., they are ossified in a 605 mm SL specimen, UMA F10023, but not in a 472 mm SL specimen, MCZ 54167). The distal radials are smaller, irregularly shaped cartilaginous nodules that never ossify. These are the last elements of the pelvic girdle to form, not being found in specimens smaller than 42.3 mm TL. Sewertzoff (1926a, fig. 11) figured a single specimen of *P. kaufmanni* in which he also found a series of elements distal to the distal radials (= his terminal radials), which he considered an atavistic variation; no such condition was discovered here, and it has not been reported by any other workers.

The pelvic fins are roughly triangular when viewed in dorsal view. The posterior medial edge of the fin is curved dorsally where it meets the body. As with all other fins, the pelvic fin rays of *A. brevirostrum* are far more numerous than are the supporting skeletal elements (Table 7).

Scutes

As in all extant acipenserids, *A. brevirostrum* possesses five longitudinal rows of large bony scutes (Fig. 97): a single median dorsal row (Figs. 98, 99) and paired lateral (Figs. 100–103) and ventral (Figs. 104, 105) rows (Table 8). In addition, there are scutes of irregular shape and number posterior to the dorsal fin (Fig. 106; Table 8) and anterior and posterior to the anal fin (Fig. 107). The scutes of *Acipenser* have previously been described and illustrated by Kosmak (1895), Sewertzoff (1926b), Jollie (1980), and Hilton and Bemis (1999). Scutes are distinguished from basal fulcra in that they are bony plates that form as a single element that are not immediately associated with a fin, whereas fulcra form in close association with the leading edge of a fin (e.g., Hilton, 2004). This differs from other recent definitions of these structures (e.g., Arratia, 2008, 2009) but is consistent with our other recent studies of acipenseriform morphology and systematics (e.g., Grande & Bemis, 1991, 1996; Bemis et al., 1997; Hilton & Grande, 2006; Hilton & Forey, 2009). There may be some evolutionary relationship between fin rays, fulcra, and dorsal scutes, and †*Priscosturion* offers a potential intermediate condition. In this taxon, the fin rays of the dorsal fin seamlessly grade into a series of larger dorsal scutes that continues anteriorly to meet the skull roof (Grande & Hilton, 2006, fig. 24).

The external surface of all scutes is heavily ornamented in adults so that the exposed portion has an irregular honeycomb appearance, with the comb being variably shaped, sized, and positioned (similar to the ornamentation of all other superficial dermal bones in sturgeons). In general, lateral and ventral scutes are lightly ossified around their margins, particularly in large specimens. All scutes undergo significant ontogenetic change in shape (e.g., they possess a sharp, recurved spine on their external surface in juveniles, whereas the adult has only a slight crest or ridge) and position (i.e., overlapping in juveniles and well spaced apart in adults). There is also significant individual variation in the shape (cf. those of the anterior and posterior parts of the dorsal series; Fig. 98) and degree of ossification (e.g., Hilton & Bemis, 1999, fig. 6) of the scutes within all series.

In our sample, the series of dorsal scutes of *A. brevirostrum* comprises 9 to 12 elements in the adult, including the anteriormost scute, which becomes incorporated into the skull roof. The anterior margin of the dorsal scutes, particularly of the more anterior scutes in the series, bears an unornamented point in the midline of the element, which is covered by skin in the adult. The dorsal scutes develop as a series in the large dorsal fin fold, which extends from the base of the skull to the position of the developing dorsal fin. Unmineralized dorsal scutes are visible in cleared and stained specimens as small as 20.5 mm TL. As Findeis (1993) found for *Scaphirhynchus*, in *A. brevirostrum* all dorsal scutes appear to develop nearly simultaneously. In only a single specimen in our series (21.9 mm TL) did we find only part of the dorsal scute series ossified (weakly stained with alizarin), and in this specimen only the scutes in the posterior portion of the series had completely ossified, suggesting a posterior-to-anterior direction of development of the dorsal scute series. The dorsal series of scutes is completely developed by 24.8 mm TL in *A. brevirostrum*. In *A. ruthenus*, there is definitely a posterior-to-anterior direction of dorsal scute development, though the scutes appear to develop over a much broader size range (pers. obs.; R. Britz, pers. comm.) than we found for *A. brevirostrum*.

The 24 to 29 lateral scutes (in our sample) of *A. brevirostrum* are roughly diamond shaped, as in other acipenserids. The lateral scutes are the last series to develop and form in an anterior-to-posterior direction (the first three scutes were first observed as tubular ossifications of the lateral line sensory canal in a 27.6 mm TL specimen). In adults, there is a slight ridge or crest on the external surface along the short axis of the lateral scutes that corresponds to the sharp thorn-shaped ridge present in juveniles; this thorn-like process may persist in large juveniles in *A. brevirostrum*. A well-developed rounded projection from the anterior margin is particularly well developed in the elements of the anterior half of the series of lateral scutes. The external surface of the lateral scutes, as with other dermal bones, is heavily ornamented. The anterior margin of the anterior lateral scutes, however, is covered by skin and remains unornamented. The lateral line sensory canal passes through each lateral scute near the middle of the element along its short axis. The canal opens on the internal surface of the scute posteriorly; its anterior opening may exit the bone on either the internal (most often) or the external surfaces. Between adjacent scutes, an ossified tube carries the sensory canal (Fig. 108).

The ventral scutes are the most variably shaped of the three main series of scutes (i.e., dorsal, lateral, or ventral). The ventral series comprises seven to nine elements in *A. brevirostrum*; these develop later than the dorsal series but before the lateral series. The first ventral scutes to form are in the middle of the series (e.g., two or three ventral scutes were found on a 26.6 mm TL specimen positioned posterior to the adpressed pectoral fin); the series is completed posterior to these first scutes and then finally the anterior scutes are added. The full series is present in a specimen 51.6 mm TL. The anteriormost ventral scute of *A. brevirostrum* is distinctly shaped, with an anteroventral extension. The middle scutes in the ventral series resemble one another in their overall shape (Figs. 104, 105), although the more posterior ones are slightly more elongate. The posteriormost ventral scute is also distinctive in shape in that its vertical axis is the main axis of the scute, whereas the horizontal axis is longer than the

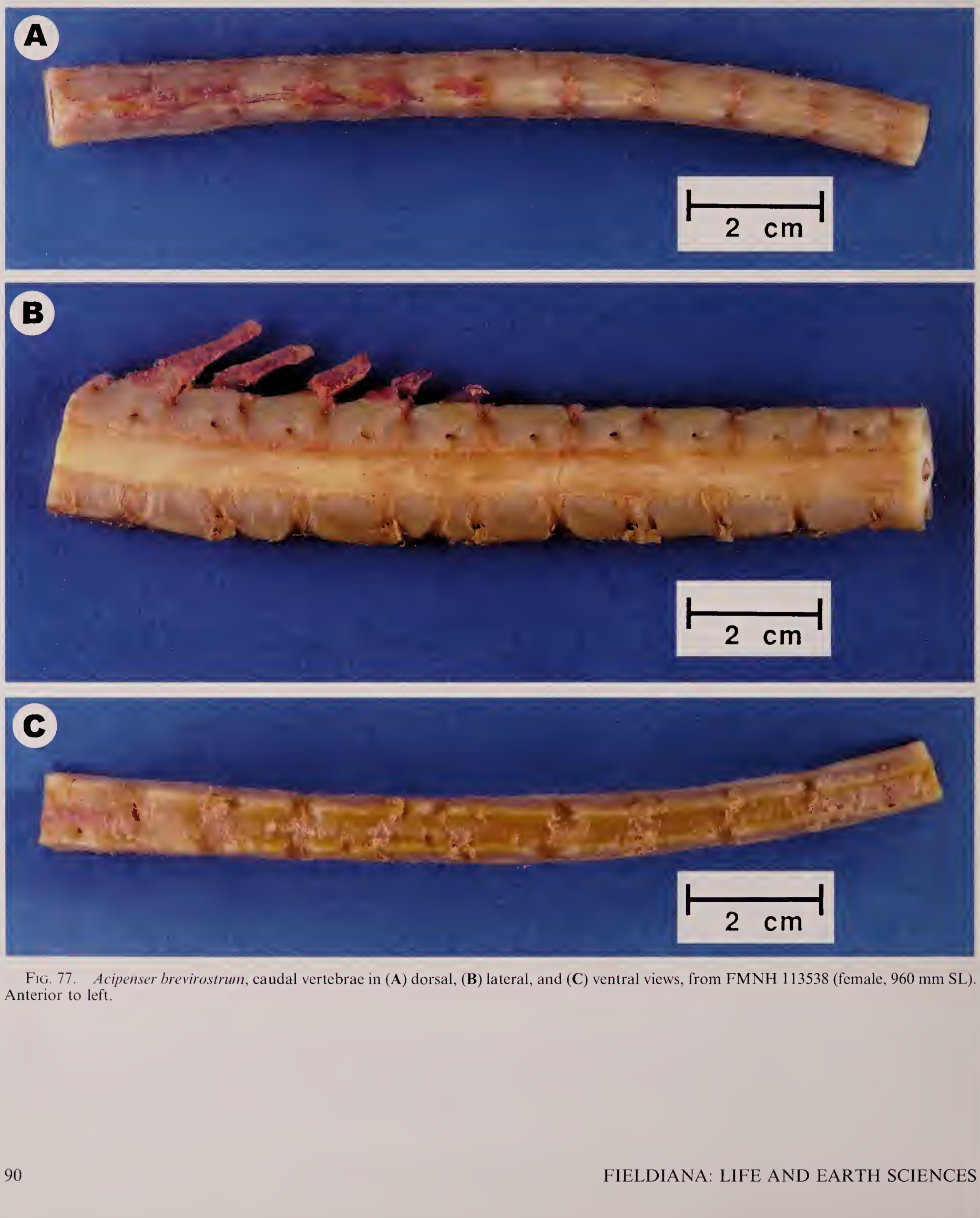


FIG. 77. *Acipenser brevirostrum*, caudal vertebrae in (**A**) dorsal, (**B**) lateral, and (**C**) ventral views, from FMNH 113538 (female, 960 mm SL). Anterior to left.

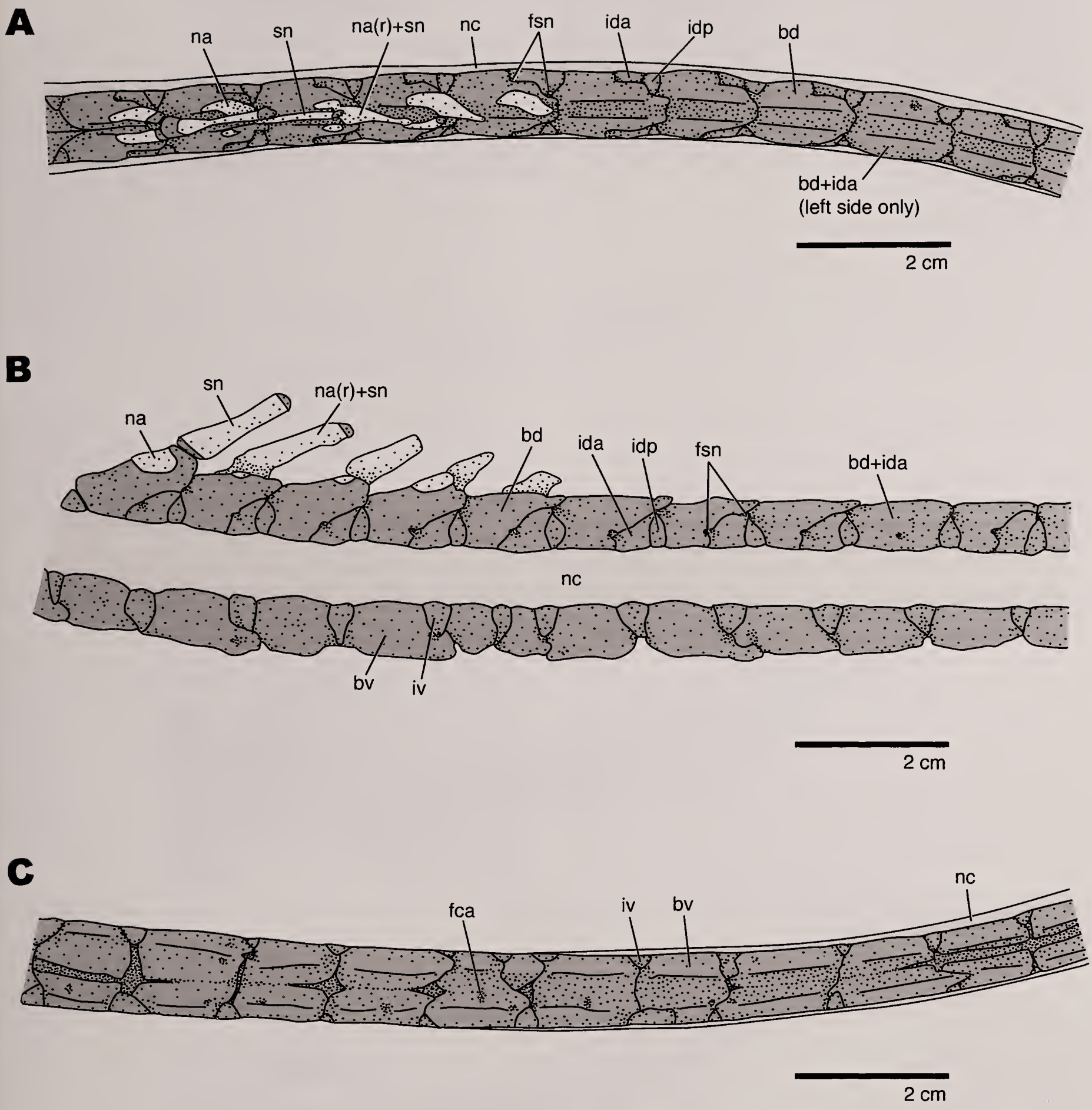


FIG. 78. *Acipenser brevirostrum*, caudal vertebrae in (**A**) dorsal, (**B**) lateral, and (**C**) ventral views. Line drawing of Figure 78. Abbreviations found on pages 8–9.

TABLE 4. Fin measurements and ratios for a growth series of *Acipenser brevirostrum*.

Specimen no. (SL)	Dorsal fin base (as %SL)	Anal fin base (as %SL)	Dorsal–to–anal fin base ratio	Dorsal lobe caudal fin (as %SL)	Ventral lobe caudal fin (as %SL)
VIMS 12101 (no SL)	3.3 mm (—)	1.8 mm (—)	1.8:1	11.1 mm (—)	3.0 mm (—)
VIMS 12082 (no SL)	4.2 mm (—)	2.7 mm (—)	1.6:1	13.2 mm (—)	6.7 mm (—)
FMNH 112215 (50.9 mm)	5.5 mm (11%)	2.1 mm (4%)	2.6:1	12.8 mm (25%)	5.7 mm (11%)
VIMS 12086 (71.1 mm)	6.6 mm (9%)	3.5 mm (5%)	1.9:1	20.8 mm (29%)	8.5 mm (12%)
FMNH 112918 (80.0 mm)	8.0 mm (10%)	4.1 mm (5%)	2:1	20.4 mm (26%)	10.3 mm (13%)
FMNH 112916 (85.5 mm)	7.4 mm (9%)	3.7 mm (4%)	2:1	27.4 mm (32%)	11.4 mm (13%)
FMNH 112917 (104.3 mm)	9.7 mm (9%)	6.9 mm (7%)	1.4:1	33.3 mm (32%)	12.8 mm (12%)
VIMS 12087 (251 mm)	25.6 mm (10%)	16.5 mm (7%)	1.6:1	92.1 mm (37%)	49.2 mm (20%)
MCZ 54167 (472 mm)	45 mm (10%)	32 mm (7%)	1.4:1	116 mm (25%)	81 mm (17%)
FMNH 117461 (640 mm)	75 mm (12%)	42 mm (7%)	1.8:1	185 mm (29%)	87 mm (14%)
ANSP 16953 holotype (690 mm)	51 mm (est.) (7%)	43 mm (est.) (6%)	1.2:1	125 mm (est.) (18%)	79 mm (11%)
FMNH 112212 (710 mm)	82 mm (12%)	39 mm (5%)	2.1:1	210 mm (30%)	115 mm (16%)
FMNH 112913 (755 mm)	82 mm (11%)	44 mm (6%)	1.9:1	152 mm (20%)	109 mm (14%)
UMA F10578 (899 mm)	85 mm (9%)	50 mm (6%)	1.7:1	200 mm (22%)	118 mm (13%)
FMNH 113538 (960 mm)	109 mm (8%)	67 mm (7%)	1.6:1	205 mm (21%)	145 mm (15%)

vertical axis in the more anterior ventral scutes. The lateral surfaces of all ventral scutes are heavily ornamented, except for the anterior regions of the anterior scutes, which are covered by a thick layer of skin and are thus unornamented (Fig. 104).

We never found additional series of lateral scutes in *A. brevirostrum*. In specimens of *A. medirostris*, we observed series of ventrolateral scutes (i.e., series of scutes between the lateral and ventral rows), ranging from a well-developed series to just a few isolated scutes (e.g., CAS 36968). These scutes are smaller than those found in the typical five rows of scutes but have a distinctive scute-like form with a sharp medial spine. A row of scutes between the dorsal and lateral series also is frequently seen in specimens of *A. gueldenstaedti* (CITES Identification Guide; also pers. obs.).

Typical for acipenserids, a variable number of scutes of *A. brevirostrum* occur on the dorsal and ventral surfaces of the caudal peduncle between the dorsal and anal fins and the caudal fin (Figs. 106, 107) as well as between the anus and the anterior margin of the anal fin (Fig. 107). The number of these elements was found to be the most individually variable of any series of scutes by Hilton and Bemis (in press); they are also highly individually variable in shape. Scutes on the caudal peduncle (except for the lateral scutes) are never as pronounced in their development as in other sturgeon species (e.g., *A. oxyrinchus* or the extreme condition of †*Priscosturion* and *Scaphirhynchus*); see page 153 for discussion of characters related to caudal peduncle armor in sturgeons.

Scales

In addition to scutes described above, the postcranial exoskeleton of Acipenseridae comprises three types of squamation: 1) bony platelets in the skin between the rows of scutes, 2) rhomboid caudal scales, and 3) round-based scales associated with the internal surface of the pectoral girdle.

The body squamation of *A. brevirostrum*, like that of other acipenserids, consists of small, irregularly shaped bony elements typically associated with denticles scattered throughout the skin between the scutes. Reflective of their structure, Kosmak (1895) referred to the body squamation as "derm-denticles" (although he also included the rhomboid caudal scales in this category of scales). There is much individual variation in the shape and size of these scales, ranging from isolated denticles or denticles with only a slightly expanded base to greatly enlarged plates of bone with many denticles on their surfaces. In some specimens of *A. brevirostrum*, the body squamation forms a nearly continuous scale jacket, whereas in most specimens the

TABLE 5. Meristic data of the caudal fin and skeleton of *Acipenser brevirostrum*. Numbers in brackets indicate number of lightly mineralized fin rays, none of which are segmented.

Specimen no. (SL)	Rudimentary: segmented caudal fin rays (no. branched)	Dorsal caudal fulcra	Rows of rhomboid caudal scales
VIMS 12101 (no SL)	0 (0)	1	0
VIMS 12082 (no SL)	[27] (0)	3	0
FMNH 112215 (50.9 mm)	iii:54 (0)	6	7
VIMS 12086 (71.1 mm)	ii:63	16	10
FMNH 112918 (80.0 mm)	ii:58 (0)	19	9
FMNH 112916 (85.5 mm)	ii:55 (0)	17	9
FMNH 112917 (104.3 mm)	i:72 (0)	22	9
VIMS 12087 (251 mm)	i:79 (17)	34	11
MCZ 54167 (472 mm)	o:75 (51+)	27	10
FMNH 117461 (640 mm)	o:83 (68)	29	11
ANSP 16953 holotype (690 mm)	?:62+ (52+)	30+	10
FMNH 112212 (710 mm)	ii:70+	23+	10
FMNH 112913 (755 mm)	o:60+ (48+)	24	10
UMA F10578 (899 mm SL)	o:59 (45)	34	10
FMNH 113538 (960 mm)	o:55 (48)	25+	11

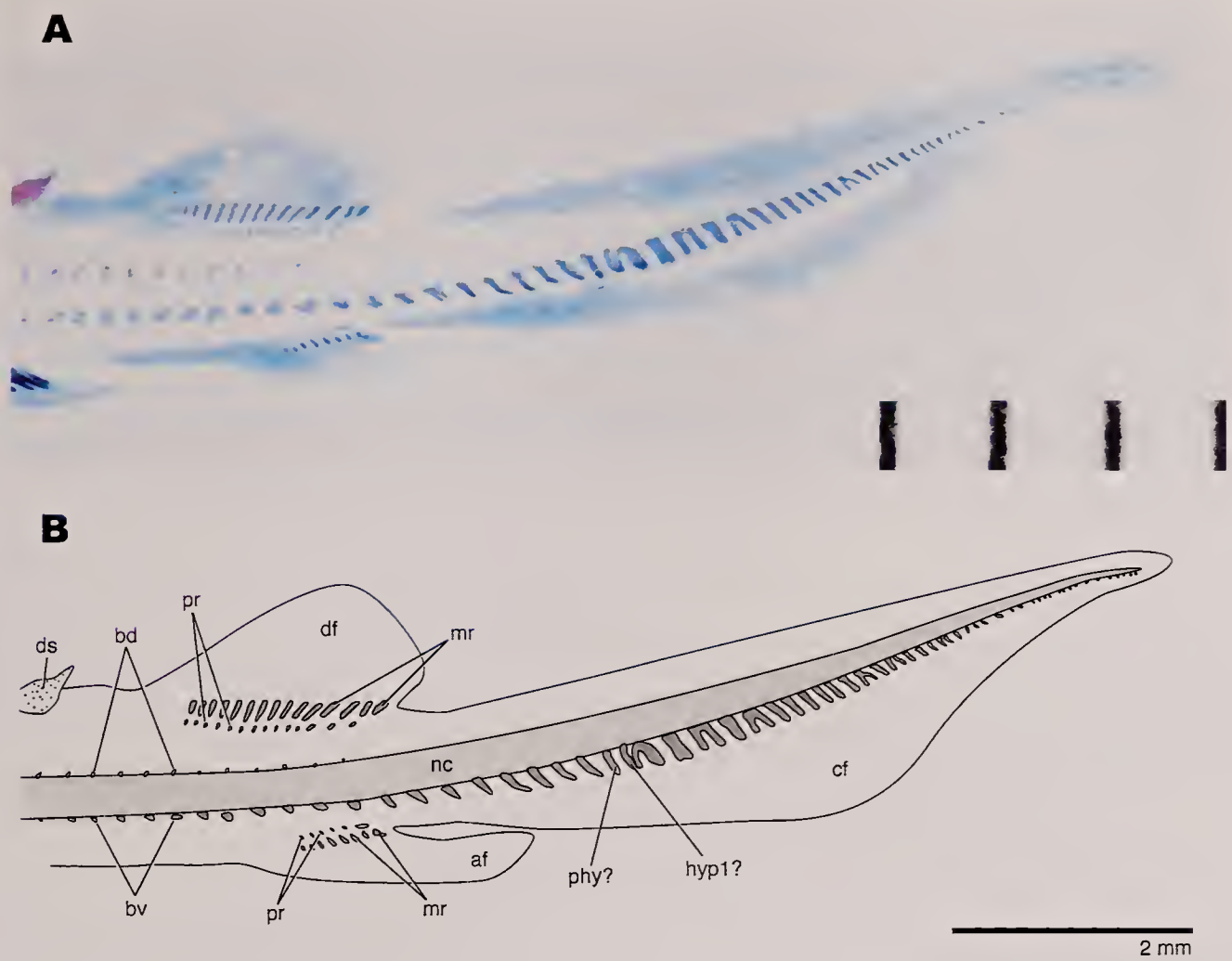


FIG. 79. *Acipenser brevirostrum*, caudal region in lateral view, showing vertebrae and dorsal, anal, and caudal fins and supports at an early stage of development, from VIMS 12079 (23.8 mm TL). (**A**) Photograph and (**B**) line drawing. Anterior to left. Abbreviations found on pages 8–9.

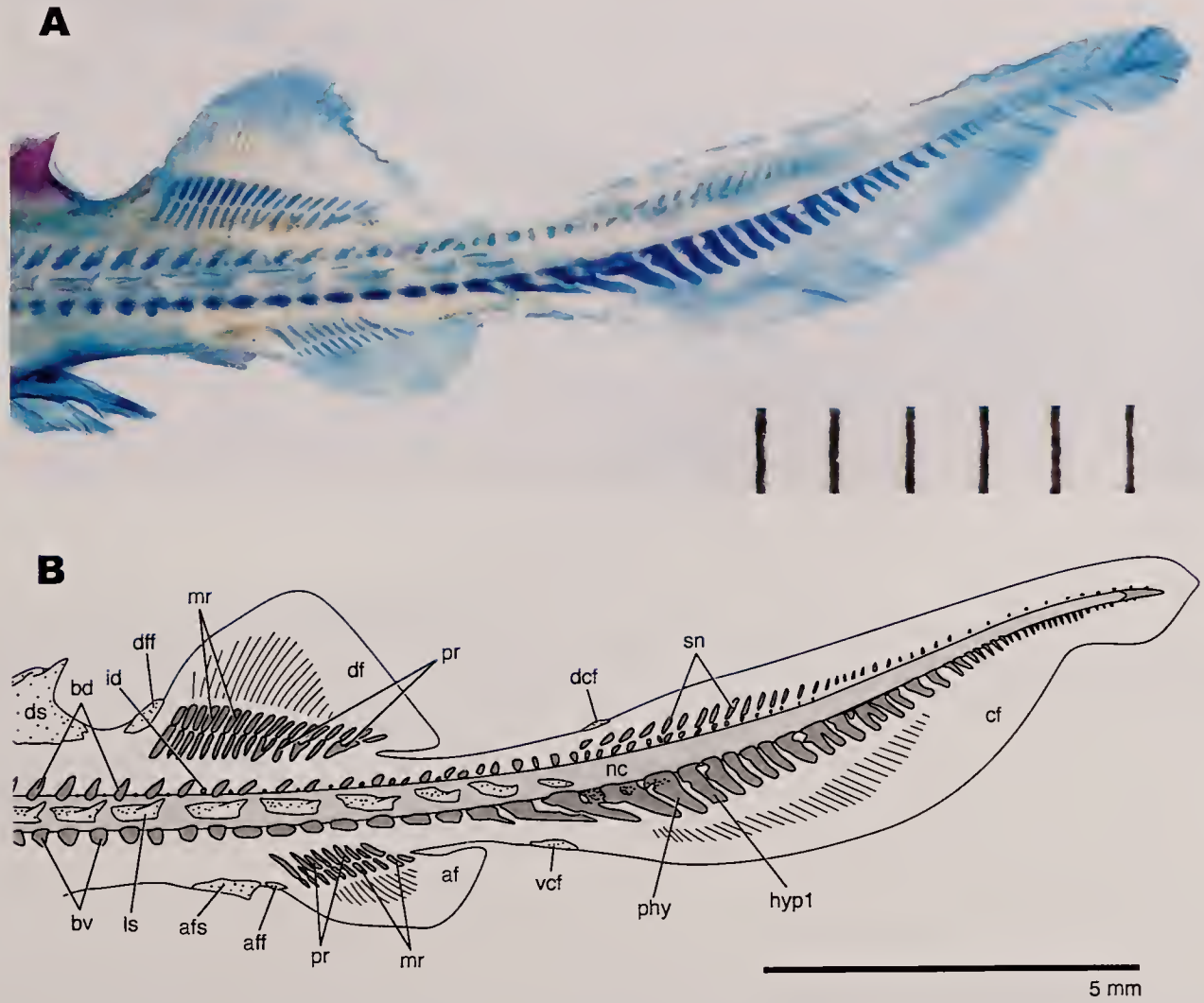


FIG. 80. *Acipenser brevirostrum*, caudal region in lateral view, showing scutes, vertebrae and dorsal, anal, and caudal fins and supports at an early stage of development, from VIMS 12089 (41.6 mm TL). (**A**) Photograph and (**B**) line drawing. Anterior to left. Abbreviations found on pages 8–9.

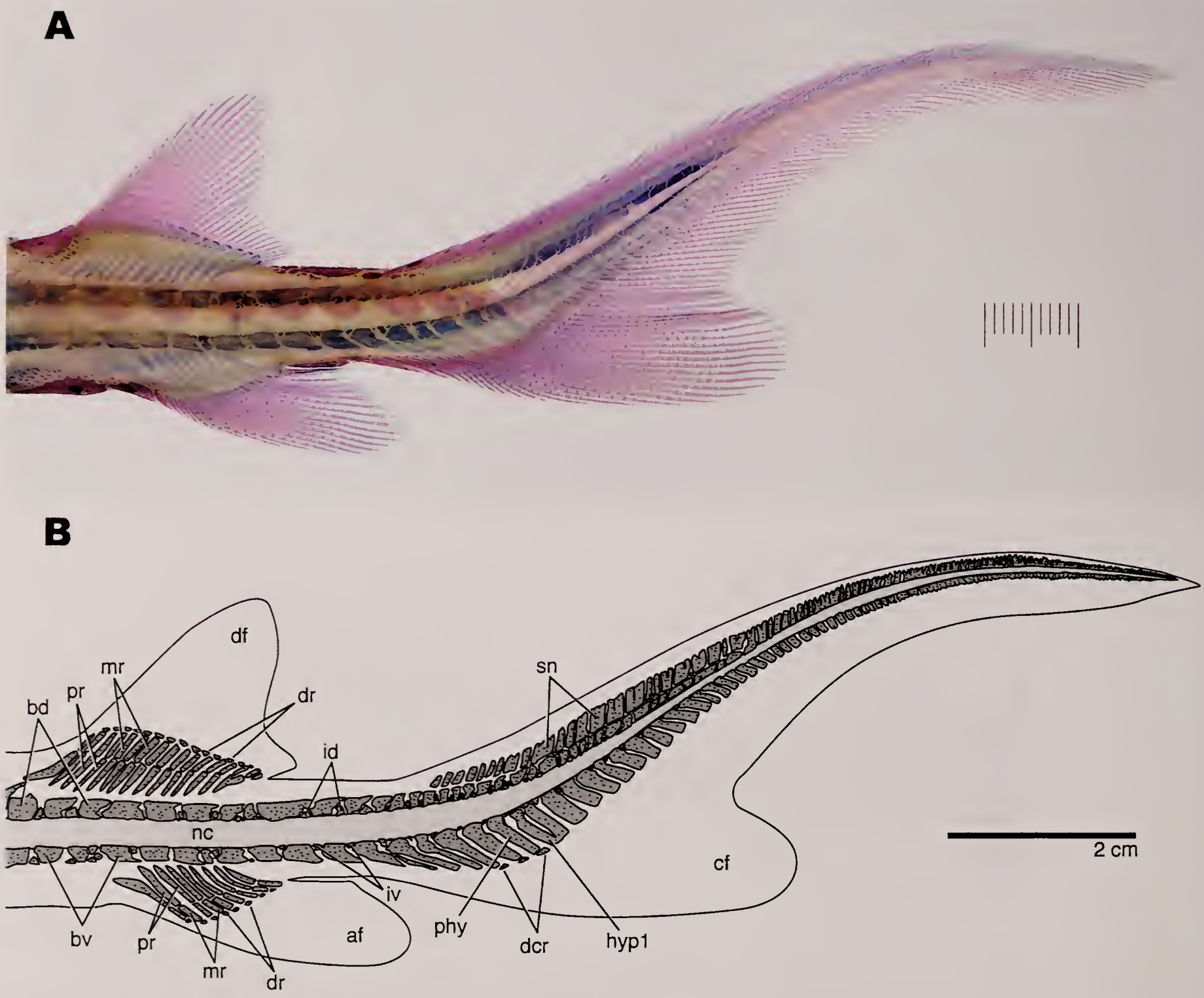
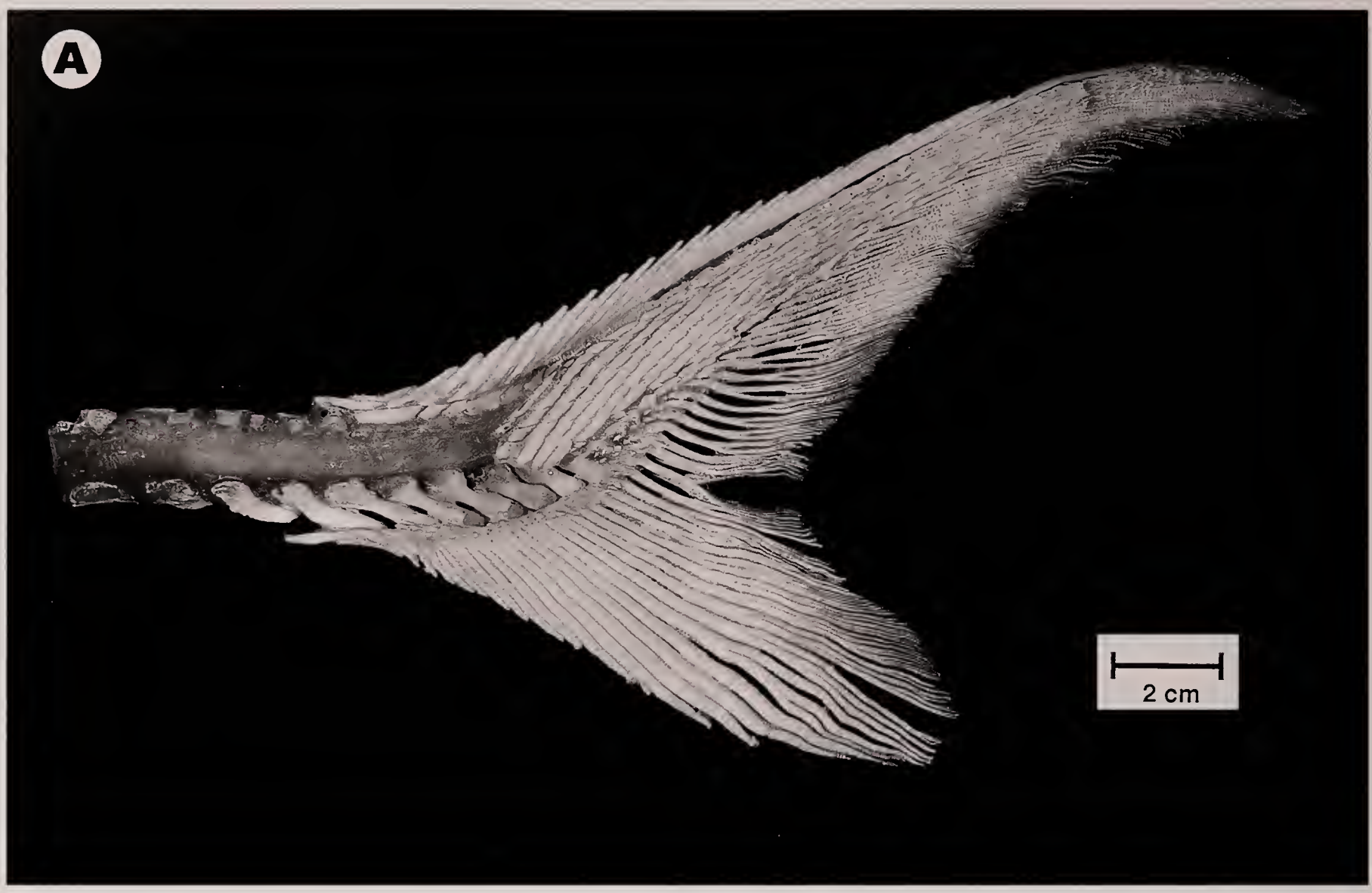


FIG. 81. *Acipenser brevirostrum*, caudal region in lateral view, showing vertebrae and dorsal, anal, and caudal fins and supports at an early stage of development with rhombic caudal scales and scutes dissected away, from VIMS 12087 (251 mm SL); right side, image reversed. (**A**) Photograph and (**B**) line drawing. Anterior to left. Abbreviations found on pages 8–9.

FIG. 82. *Acipenser brevirostrum*, internal supports of caudal fin in lateral view, from FMNH 113538 (female, 960 mm SL). **(A)** Photograph and **(B)** line drawing. In photo, bone is stained red, and cartilage appears white; in drawing, bone is white, and cartilage is gray. Anterior to left. Abbreviations found on pages 8–9.



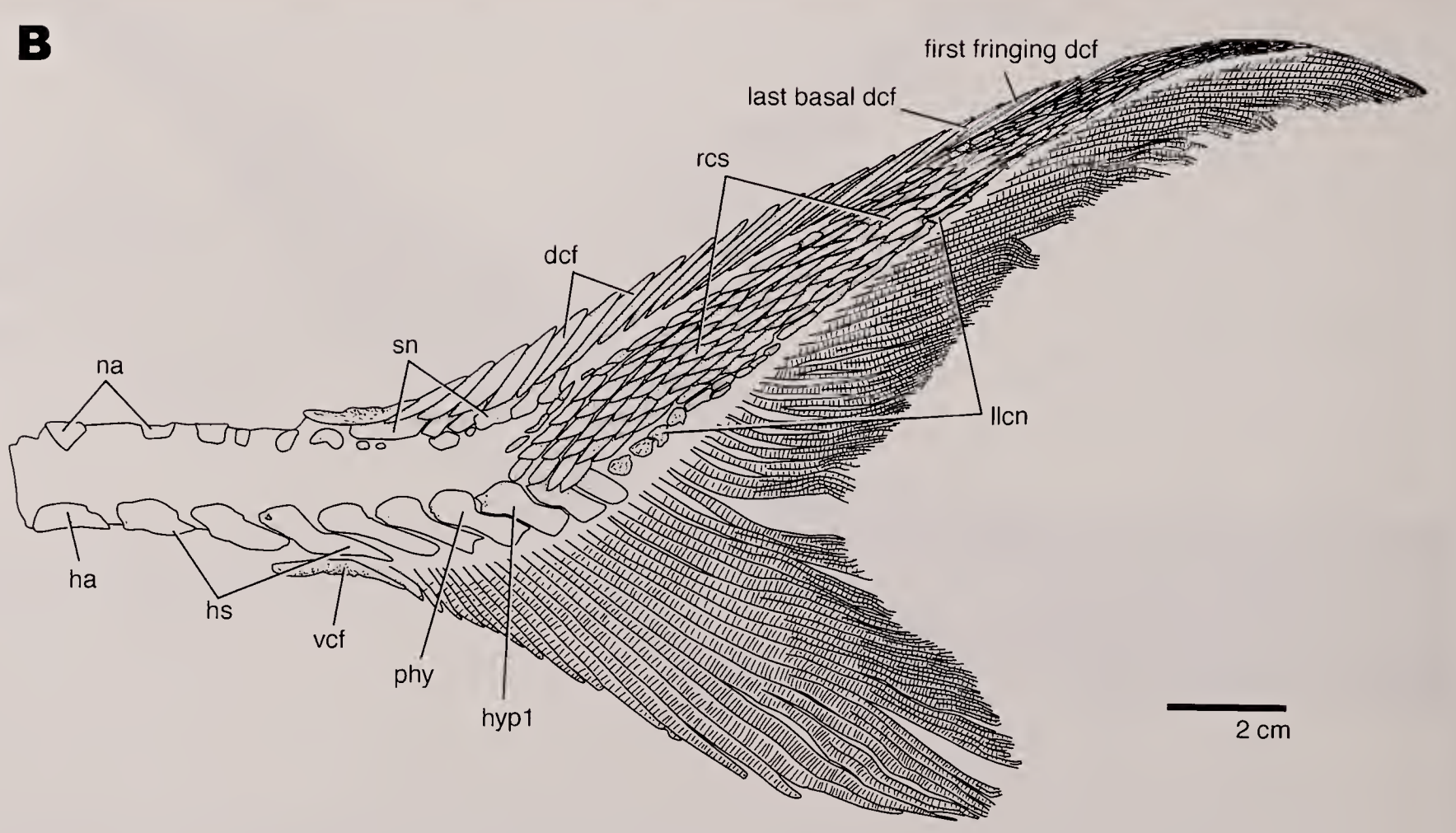


FIG. 83. *Acipenser brevirostrum*, ossifications of the caudal fin and supporting skeleton in lateral view, from UMA F10578 (male, 899 mm SL). (**A**) Photograph and (**B**) line drawing. Anterior to left. Abbreviations found on pages 8–9.

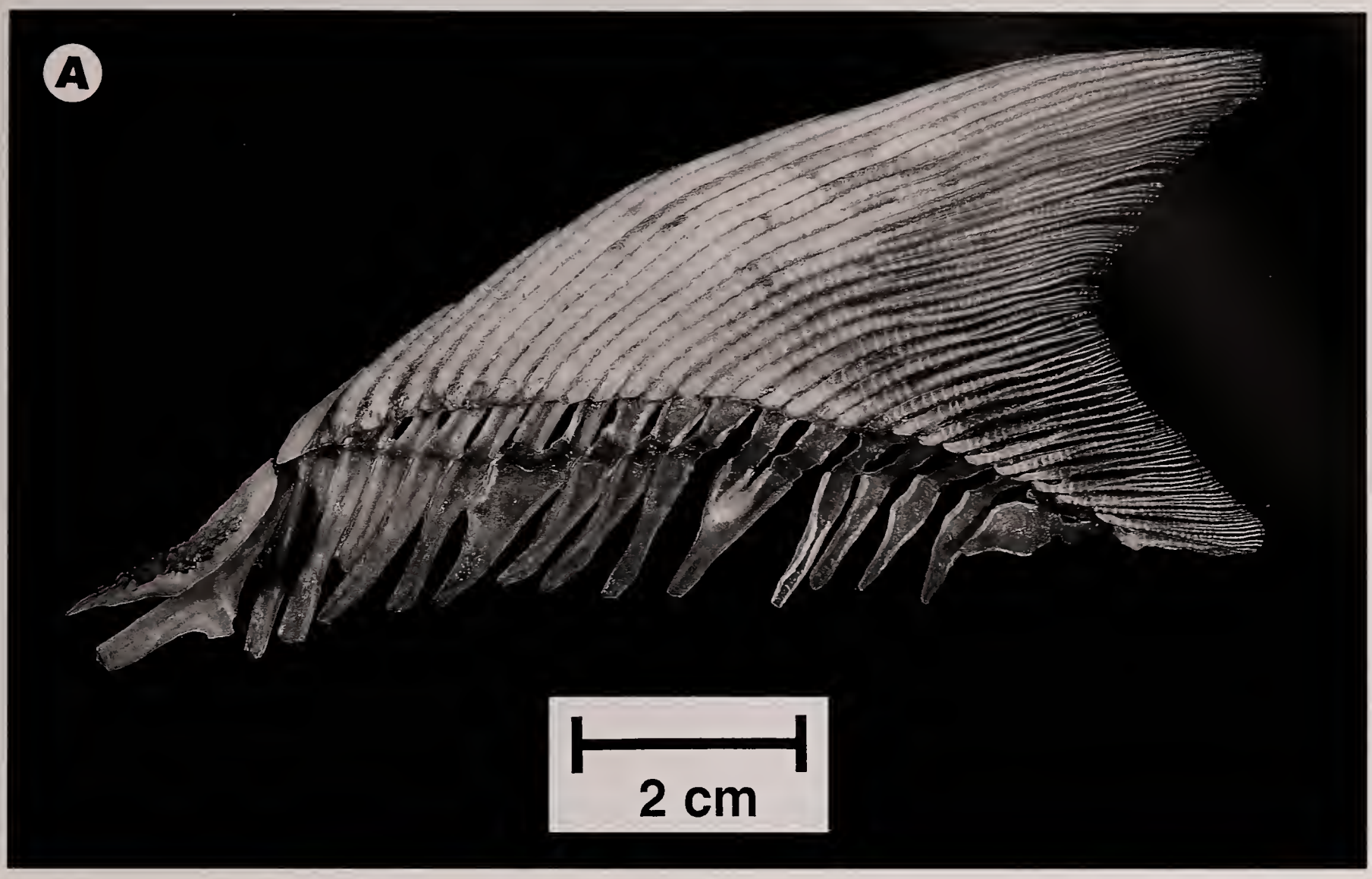


FIG. 84. *Acipenser brevirostrum*, dorsal fin and skeletal supports in lateral view, from UMA F10579 (female, 880 mm SL). (**A**) Photograph and (**B**) line drawing. Anterior to left. Abbreviations found on pages 8–9.

FIG. 85. *Acipenser brevirostrum*, dorsal fin skeletal supports in lateral view, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing. In photo, bone is stained red, and cartilage appears white; in drawing, bone is white, and cartilage is gray. Anterior to left. Abbreviations found on pages 8–9.

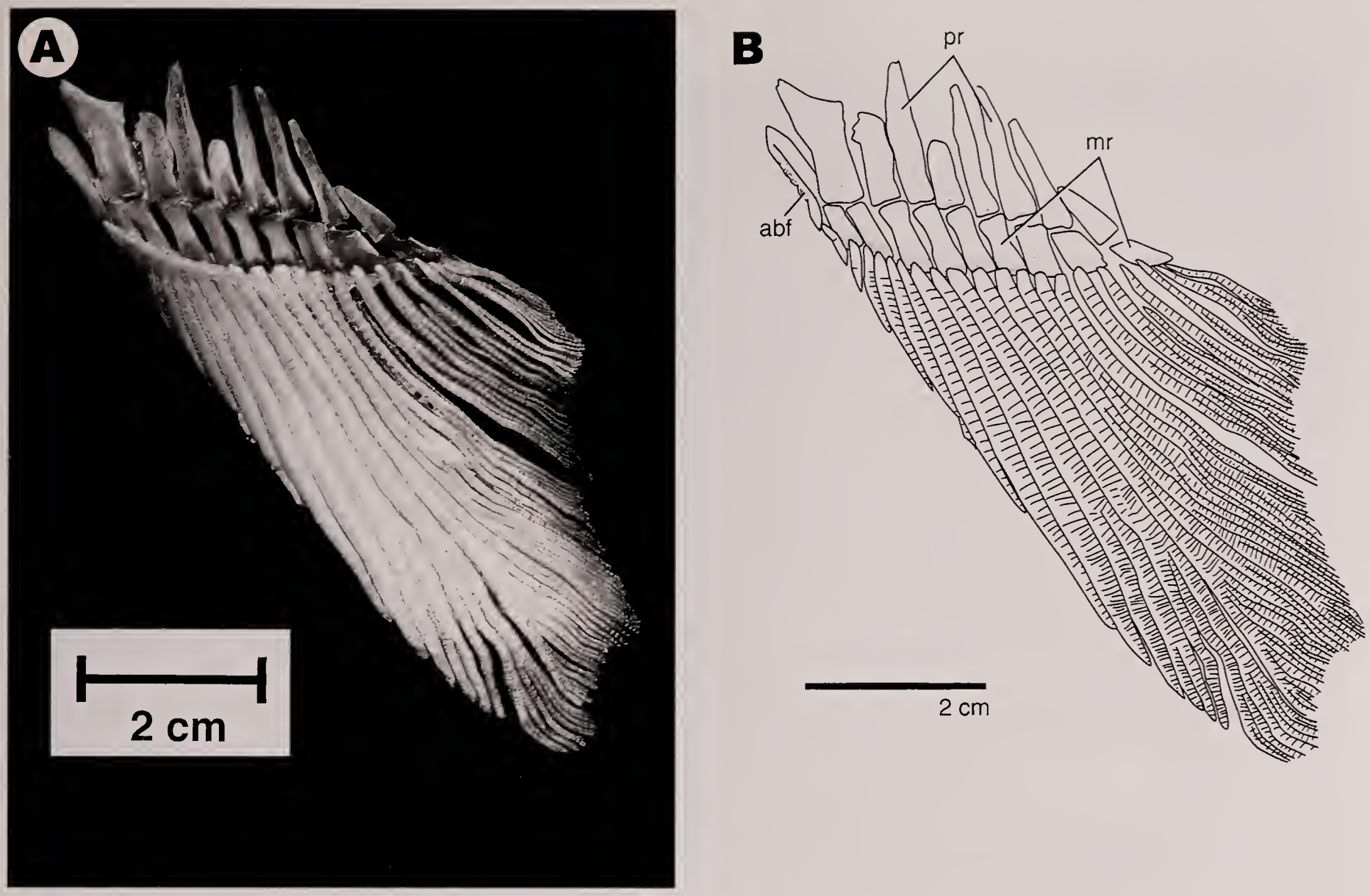


FIG. 86. *Acipenser brevirostrum*, anal fin and skeletal supports in lateral view, from UMA F10578 (male, 899 mm SL). (**A**) Photograph and (**B**) line drawing. Anterior to left. Abbreviations found on pages 8–9.

body, scales are well spaced; the degree of coverage between the scutes appears to be individually variable (e.g., Figs. 108, 109A).

The lateral surfaces of the dorsal lobe of the caudal fin of *A. brevirostrum*, as in all other acipenserids and most basal actinopterygians, are armored by a series of rhomboid caudal scales (Fig. 109; see Smith, 1956; Hilton, 2004). These are thick, bony scales organized in overlapping rows. The more posteriorly positioned rhomboid caudal scales tend to be more elongate than those positioned more anteriorly. The rhomboid caudal scales also support lines or patches of denticles that may be fused to the scales (Figs. 109D, 110). similar to the body squamation.

Extant acipenserids (other than *Scaphirhynchus* and *Pseudoscaphirhynchus*), polyodontids. and †peipiaosteids have irregularly arranged round-based scales (Grande & Bemis,

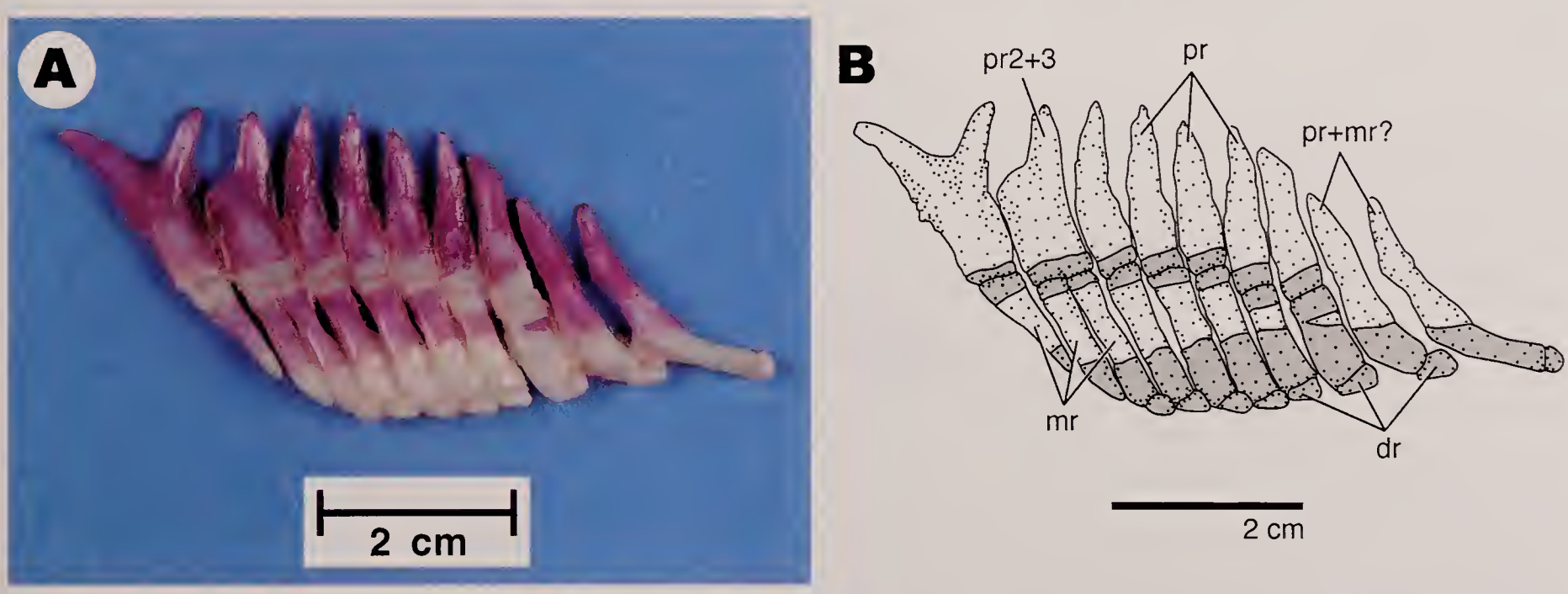


FIG. 87. *Acipenser brevirostrum*, anal fin skeletal supports in lateral view, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing. In photo, bone is stained red, and cartilage appears white; in drawing, bone is white, and cartilage is gray. Anterior to left. Abbreviations found on pages 8–9.

TABLE 6. Meristic data of dorsal and anal fin rays and pterygiophores for *Acipenser brevirostrum*. Numbers in brackets indicate number of lightly mineralized fin rays, none of which are segmented.

Specimen no. (SL)	Rudimentary: segmented dorsal fin rays (no. branched)	Dorsal fin proximal radials (no. ossified)	Dorsal fin middle radials (no. ossified)	Rudimentary: segmented anal fin rays (no. branched)	Anal fin proximal radials (no. ossified)	Anal fin middle radials (no. ossified)
VIMS 12101 (no SL)	0 (0)	? (0)	18 (0)	0 (0)	? (0)	10 (0)
VIMS 12082 (no SL)	[17] (0)	15 (0)	16 (0)	[2] (0)	11 (0)	10 (0)
FMNH 112215 (50.9 mm)	iv:36 (0)	17 (0)	16 (0)	iv:17 (0)	7 (0)	9 (0)
VIMS 12086 (71.1 mm)	o:29 (0)	13 (0)	16 (0)	iii:19 (0)	9 (0)	9 (0)
FMNH 112918 (80.0 mm)	i:31 (0)	17 (0)	18 (0)	i:23 (0)	10 (0)	11 (0)
FMNH 112916 (85.5 mm)	iii:27 (0)	12 (0)	18 (0)	iii:17 (0)	? (0)	9 (0)
FMNH 112917 (104.3 mm)	i:30 (0)	15 (0)	17 (0)	iii:22 (0)	13 (0)	13 (0)
VIMS 12087 (251 mm)	i:31 (8)	15 (0)	17 (0)	ii:23 (8)	10 (0)	11 (0)
MCZ 54167 (472 mm)	o:35 (25)	16 (12)	? (0)	i:24 (13)	9 (8)	? (?)
FMNH 117461 (640 mm)	i:38 (27)	? (?)	? (?)	o:24 (13)	? (?)	? (?)
ANSP 16953 holotype (690 mm)	ii:31 (23+)	? (?)	? (?)	ii:20 (15)	? (?)	? (?)
FMNH 112212 (710 mm)	i:36 (26)	? (?)	13 (13)	ii:18 (11)	8+ (8+)	8+ (8+)
FMNH 112913 (755 mm)	i:34 (26)	15* (13)	13* (9)	i:22 (14)	9 (9)	9 (9)
UMA F10578 (899 mm)	o:33 (26)	13 (13)	15 (15)	i:20 (13)	8 (8)	9 (9)
FMNH 113538 (960 mm)	ii:32 (26)	16** (15)	11** (11)	i:20 (13)	9* (9)	8* (8)

* Posteriormost two pterygiophores have single element in position of proximal and middle radials; these elements were included in proximal radial count only (e.g., see Figs. 85, 87).

** Posteriormost five pterygiophores are single elements; these elements were included in the proximal radial count only.

1991, 1996; Findeis, 1997, characters 23, 54) on the anterior (i.e., external) surface of the bony opercular wall formed by the eleithrum and clavicle (Fig. 94). In *A. brevirostrum* and many other acipenserids and polyodontids examined, these scales are found from the posttemporal region of the pectoral girdle ventral to the isthmus. In large specimens of *A. transmontanus*, similar round-based scales were also found on the internal surfaces of the subopercle and the opercular flap posterior to the pseudobranch. In *A. brevirostrum*, these scales are loosely embedded in the skin and are typically lost during preparation of dry skeletal material. These thin scales have a rounded anterior margin and posteriorly bear three or four finger-like extensions. The external surface of each scale is finely ridged (seen only with SEM; Fig. 94B, C) except for the margins of the finger-like projections, which have a smooth surface.

Systematic Analysis of Acipenseridae

Sturgeon Diversity

On pages 122–135, we present a series of figures illustrating some of the morphological diversity within the family Acipenseridae (Figs. 111–123). We follow Birstein and Bemis (1997a) in recognizing 25 valid extant species of sturgeons. Further, we follow Hilton and Grande (2006) in recognizing †*Priscosturion longipinnis* and †*Protoscaphirhynchus squamosus* as the two valid fossil acipenserid taxa (Table 9), although we echo their statement (see also Grande & Hilton, 2006) that, because it is very poorly preserved, †*P. squamosus* "should be treated as an inserted taxon (Grande & Bemis, 1998, p. 569) in future systematic analyses" (Hilton & Grande, 2006, p. 675). As pointed out by Hilton and Grande (2006), although the family Acipenseridae can be recognized in the fossil record for at least 85 million years (i.e., since the Late Cretaceous), species-level diversity through all this history cannot be evaluated because of the fragmentary nature of the fossils themselves (e.g., consisting largely of broken scutes and spines).

Recent Phylogenetic Analyses of Species in the Family Acipenseridae

Several recent studies have explored interrelationships within the family Aeipenseridae, and most have used molecular data sets. In this section, we briefly review these recent analyses to provide context for our phylogenetic analysis. This discussion of selected modern treatments of sturgeon interrelationships is not intended to be exhaustive. The taxonomic sampling of sturgeons has been as varied as the number of studies, ranging from narrowly focused studies of sturgeons from particular regions to more global analyses. For instance, using mitochondrial sequence data, Krieger et al. (2000; see also Krieger & Fuerst, 2002) concentrated on relationships among North American species and found support for ([{*A. transmontanus* + *A. medirostris*} {*A. brevirostrum* + *A. fulvescens*}]; the two subspecies of *A. oxyrinchus*).

Ludwig et al. (2000) presented results of two molecular analyses based on analysis of complete sequences of the cyt*b* gene of 19 aeipenserids (three species of *Scaphirhynchus*, *H. huso*, and 15 species of *Acipenser*), which served as a basis for their study of heteroplasmy within sturgeons. This data set was expanded by Ludwig et al. (2001) to include two more species of *Acipenser* (*A. schrenki* and *A. sinensis*) and the other species of *Huso* (*H. dauricus*) and was used to study genome duplication and the evolution of ploidy levels of aeipenserids. Their results, as with those of Ludwig et al. (2000), did not support the monophyly of *Acipenser* (Fig. 124A), but the relative relationships among North American sturgeons were consistent with Krieger et al. (2000). In this tree, the species of *Scaphirhynchus* formed a monophyletic group in a polytomy with *A. oxyrinchus* + *A. sturio* and a group including all other taxa studied (14 species of *Acipenser* and the two species of *Huso*). They further found a primary dichotomy between a "Pacific elade," including *H. dauricus*, *A. mikadoi*, *A. medirostris*, *A. schrenki*, *A. transmontanus*, and *A. sinensis*, and a so-called Atlantic clade that included taxa from North America (*A. brevirostrum* and *A. fulvescens*) as well as those from Europe and central Asia.

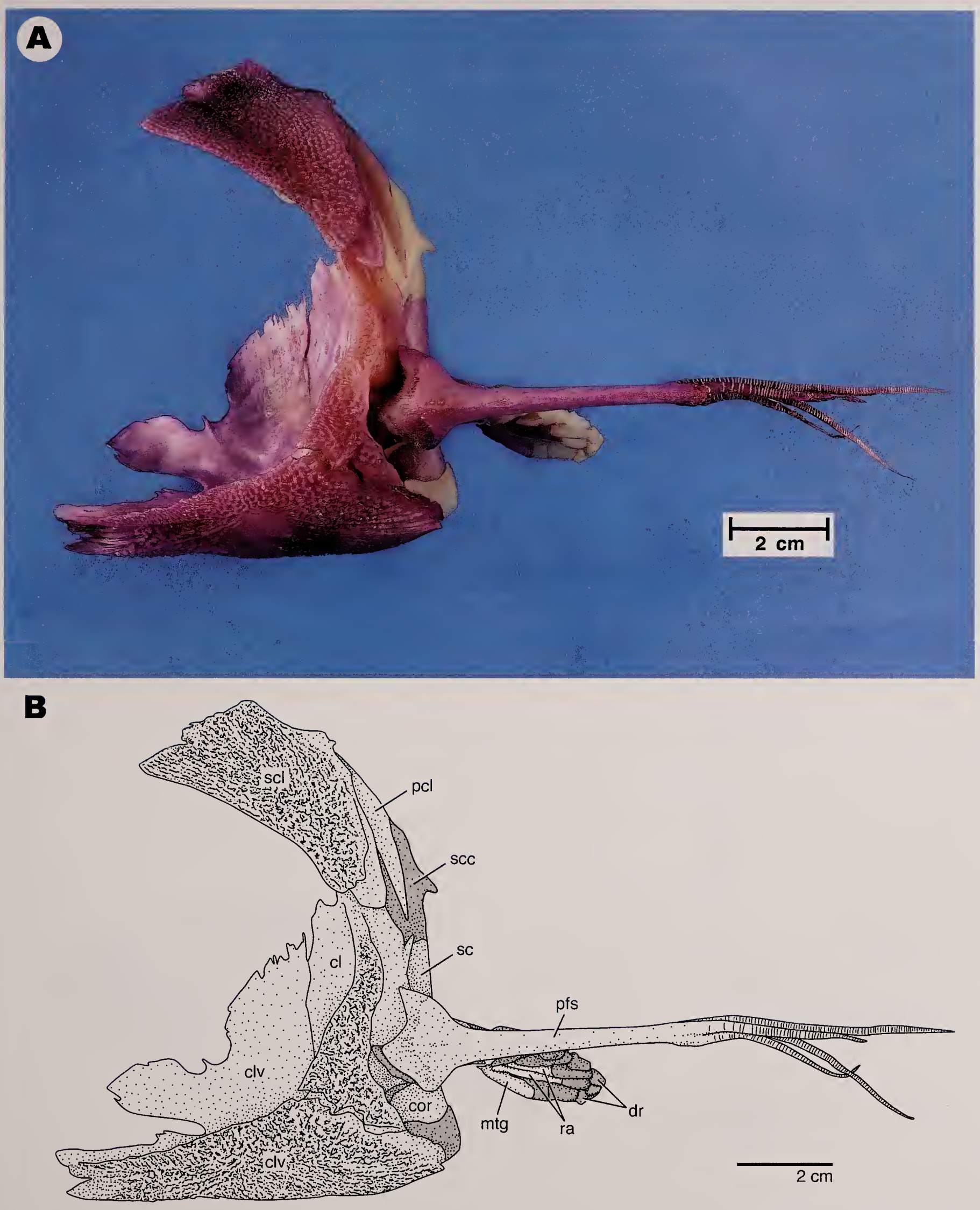


FIG. 88. *Acipenser brevirostrum*, pectoral girdle, fin supports, and fin spine in lateral view, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing. In photos, bone is stained red, and cartilage appears white; in drawings, bone is white, and cartilage is gray. Anterior to left. Abbreviations found on pages 8–9.

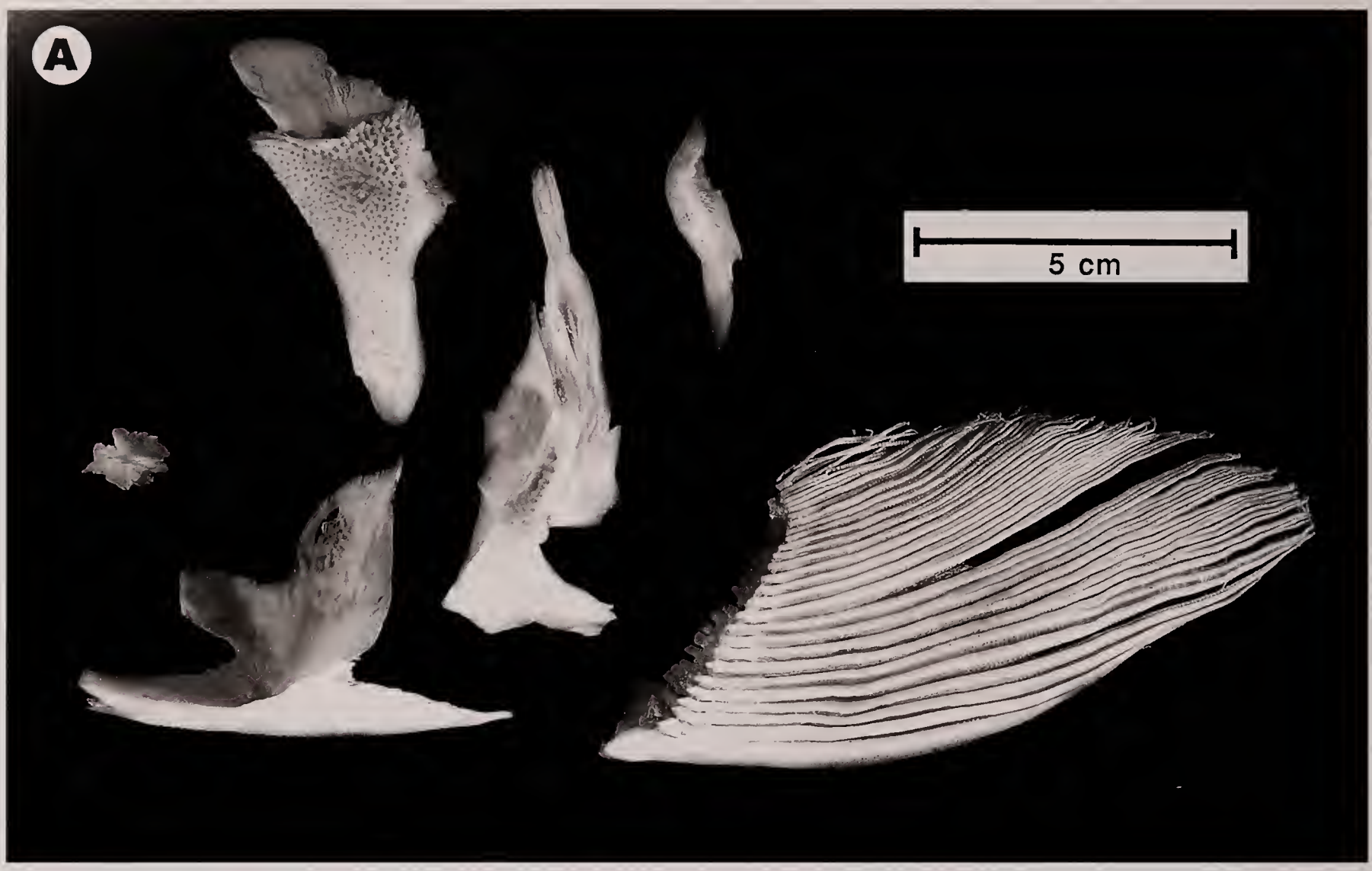


FIG. 89. *Acipenser brevirostrum*, disarticulated dermal bones of the pectoral girdle and the pectoral fin, mostly in lateral view (pectoral fin and interclavicle in dorsal view), from UMA F10431 (male, 930 mm SL). (**A**) Photograph and (**B**) line drawing. The posttemporal is fully incorporated into the skull roof and is illustrated in Figures 8, 9, and 11–14. Note that the posterior fin rays are not in natural position in this specimen. Anterior to left. Abbreviations found on pages 8–9.

TABLE 7. Meristic data of paired fins for a growth series of *Acipenser brevirostrum*. Numbers in brackets indicate number of partially mineralized fin rays, none of which are segmented.

Specimen no. (SL)	L, R pectoral fin rays (no. branched)	L, R pectoral radials (no. ossified)	Rudimentary: segmented L, R pelvic fin rays (no. branched)	L, R autogenous proximal pelvic radials (no. ossified)
VIMS 12101 (no SL)	[15, 13] (0, 0)	6, 7 (0, 0)	0, 0 (0, 0)	9, 9 (0, 0)
VIMS 12082 (no SL)	[21, 17] (0, 0)	6, 7 (0, 0)	0, 0 (0, 0)	9, 8 (0, 0)
FMNH 112215 (50.9 mm)	29, 28 (0, 0)	7, 7 (0, 0)	v:22, vi:21 (0, 0)	9, 9 (0, 0)
VIMS 12086 (71.1 mm)	33, 36 (0, 0)	6, 6 (0, 0)	i:25, i:26 (0, 0)	9, 8 (0, 0)
FMNH 112918 (80.0 mm)	37, 29 (0, 0)	8, 7 (0, 0)	teratological	teratological
FMNH 112916 (85.5 mm)	29, 27 (0, 0)	6, 6 (0, 0)	iv:24, iv:22 (0, 0)	8, 8 (0, 0)
FMNH 112917 (104.3 mm)	34, 32 (0, 0)	7, 7 (0, 0)	ii:27, i:30 (0, 0)	9, 9 (0, 0)
VIMS 12087 (251 mm)	39, 38 (9, 7)	8, 7 (0, 0)	ii:26, ii:26 (0, 0)	8, 7 (0, 0)
MCZ 54167 (472 mm)	31, 31 (30, ?)	5, 5 (2, 2)	i:25, ii:22 (16, 14)	8, 7 (0, 0)
FMNH 117461 (640 mm)	36, 35* (33, 31)	?, ? (?, ?)	o:26, i:25 (17, 15)	?, ? (?, ?)
ANSP 16953 holotype (690 mm)	?, ? (?, ?)	?, ? (?, ?)	?, ? (?, ?)	?, ? (?, ?)
FMNH 112212 (710 mm)	32, 35 (25, 29)	6, 6 4, 4	i:24, i:22 (15, 15)	7, 7 (7, 7)
FMNH 112913 (755 mm)	30, 34 (30, 34)	6, ? (6, ?)	iii:23, ii:22 (16, 16)	?, ? (?, ?)
UMA F10578 (899 mm)	30, 34 (28, 31)	5, 5 (5, 5)	iii:22, iii:24 (16, 17)	8, 7 (8, 7)
FMNH 113538 (960 mm)	27, 26 (27, 26)	?**, 5 (?, 4)	i:24, i:22 (17, 16)	8, 7 (8, 7)

* Second fin ray is branched, but the third and fourth are unbranched.
** There are two autogenous anterior radials and a large ossified plate that articulates with the metapterygium.

Zhang et al. (2000) used sequences from two mitochondrial genes (ND4L and ND4) to analyze the relationships of 10 species of sturgeons, including all the Chinese species. Their maximum parsimony analysis (Fig. 124B) recovered an Asian clade and supported the paraphyly of *Huso*, with both species of *Huso* nested within *Acipenser*.

Fontana et al. (2001) reviewed genetic literature regarding sturgeons, focusing on chromosomal evolution and molecular systematics. They presented the results of a UPGMA analysis of cyt*b* to examine the relationships of 18 species of sturgeons (Fig. 124C). As in other analyses, the relative relationships among North American species of *Acipenser*, at least, were found to be *A. oxyrinchus* ([*A. transmontanus*, *A. medirostris*] [*A. brevirostrum*, *A. fulvescens*]). However, they found the genus *Scaphirhynchus* to be the sister group of all other sturgeons except *A. sturio* + *A. oxyrinchus*. They also found *Huso* to be deeply nested within *Acipenser*.

Birstein and De Salle (1998) published an analysis of segments of three mitochondrial genes (cyt*b*, 12S rRNA, and 16S rRNA) for all species of *Acipenser*, *Huso*, and *S. albus* (Fig. 125A; see also Birstein et al., 1997a). They found *Scaphirhynchus* to be basal among extant sturgeons and *Huso* to be nested deeply within *Acipenser*. In contrast to other molecular analyses, *A. fulvescens* was found to be more closely related to *A. transmontanus* and *A. medirostris* than to *A. brevirostrum*. In 2002, Birstein et al. expanded this data set to include all sturgeon species (except *P. fedchenkoi*). *Scaphirhynchus* was again recovered as basal among all sturgeons, and a paraphyletic *Huso* was found to be nested deeply inside of *Acipenser* (Fig. 125B, C). Perhaps their most surprising result was that *Pseudoscaphirhynchus* was also found deeply nested inside of *Acipenser* as sister group to *A. stellatus* (see discussion in Hilton, 2005).

Dillman et al. (2007) sought to test the nonmonophyly of *Scaphirhynchus* + *Pseudoscaphirhynchus* and analyzed 827 base pairs of control region and 1140 base pairs of cyt*b*. As in Birstein et al. (2002), these authors also recovered a paraphyletic Scaphirhynchinae and found *A. stellatus* to be the closest relative of *Pseudoscaphirhynchus* in both parsimony and Bayesian analyses (Fig. 126A). Further, their data failed to confirm the monophyly of *S. albus*, *S. platorhynchus*, *A. gueldenstaedtii*, *A. baerii*, and the various morphs of species of *Pseudoscaphirhynchus*.

Morphological cladistic analyses of sturgeon interrelationships have lagged far behind molecular analyses, perhaps because of the widely held belief that morphological characters are incapable of resolving species-level relationships of sturgeons because of 1) intraspecific variation and 2) the conservative nature of sturgeon anatomy. In terms of character data, the most exhaustive morphological analysis of relationships within Acipenseridae presented to date was that of Findeis (1997). Others include Artyukhin (1995; see also Artyukhin, 2006; Fig. 127C) and Mayden and Kuhajda (1996; Fig. 127A), but these will not be discussed in detail here because of analytical problems of the former (although see the reworking of his data by Choudhury & Dick, 1998; Fig. 127B) and the specific focus of the latter on the relationships among species of *Scaphirhynchus*. Vasil'eva (1999, 2009) also presented results of similarity and cluster analyses of cranial morphometric data for 19 species of sturgeons. These data were found to be important for diagnoses of some species. The focus of Findeis's study was generic-level relationships and followed from his morphological description of the genus *Scaphirhynchus* (Findeis, 1993). His analysis of 69 morphological characters resulted in *Huso* being interpreted as the most basal genus within the family and *Scaphirhynchus* and *Pseudoscaphirhynchus* as sister taxa (i.e., *Huso* [*Acipenser* {*Scaphirhynchus*, *Pseudoscaphirhynchus*}]); he was unable to find characters supporting the monophyly of *Acipenser*. We use Findeis's (1997) study as the starting point for our own systematic analysis.

With the description of †*Priscosturion longipinnis*, Grande and Hilton (2006) presented a genus-level phylogenetic analysis of sturgeons that resulted in the topology †*Priscosturion* (*Huso*, *Acipenser* [*Pseudoscaphirhynchus*, *Scaphirhynchus*]). The result of *Pseudoscaphirhynchus* + *Scaphirhynchus* was likely due to taxon sampling within *Acipenser* (see discussion below). Hilton and Forey (2009), in their redescription of †*Chondrosteus acipenseroides*, analyzed a data matrix very similar to that discussed here (because of an overlap of the first author between the two studies). However, the discussion in that study was focused on the position of

FIG. 90. *Acipenser brevirostrum*, pectoral girdle, fin supports, and fin spine in medial view, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing. In photos, bone is stained red, and cartilage appears white; in drawings, bone is white, and cartilage is gray. Anterior to left (images reversed to show medial surface of elements but with anterior to left). Abbreviations found on pages 8–9.

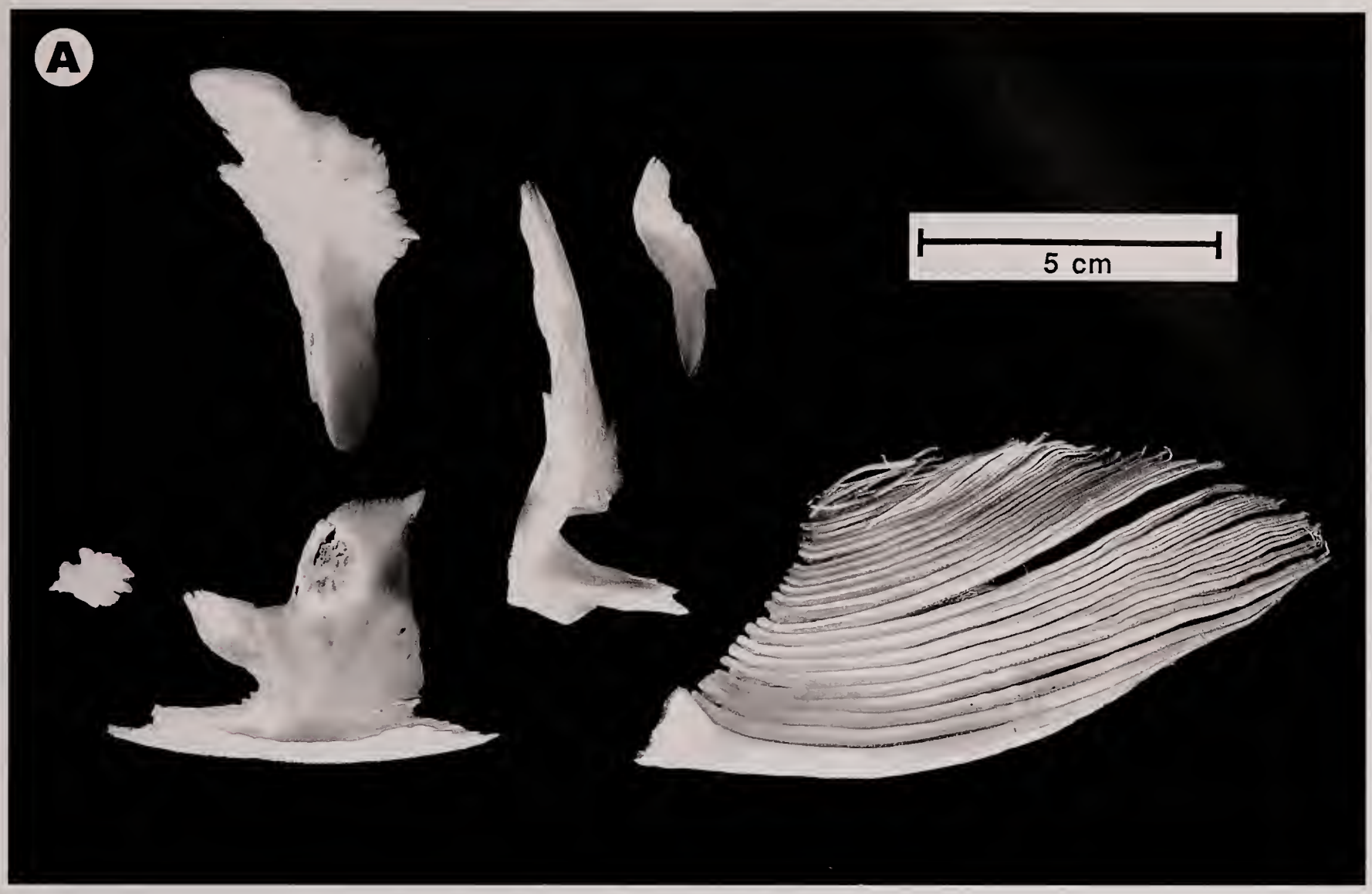


FIG. 91. *Acipenser brevirostrum*, disarticulated dermal bones of the pectoral girdle and the pectoral fin, mostly in medial view (pectoral fin and interclavicle in ventral view), from UMA F10431 (male, 930 mm SL). (**A**) Photograph and (**B**) line drawing. The posttemporal is fully incorporated into the skull roof and is illustrated in Figures 8, 9 and 11–14. Note that the posterior fin rays are not in natural position in this specimen. Anterior to left (images reversed to show medial surface of elements but with anterior to left). Abbreviations found on pages 8–9.

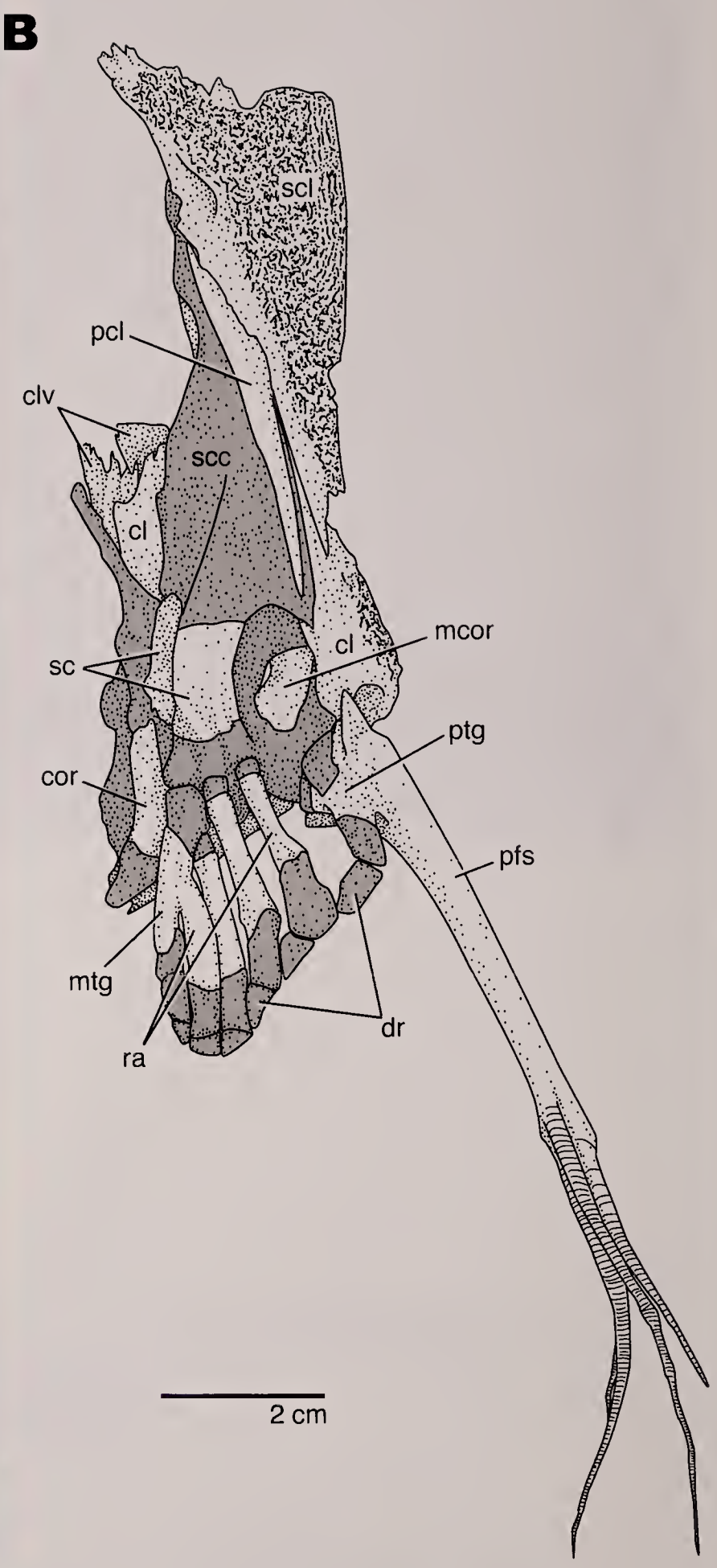
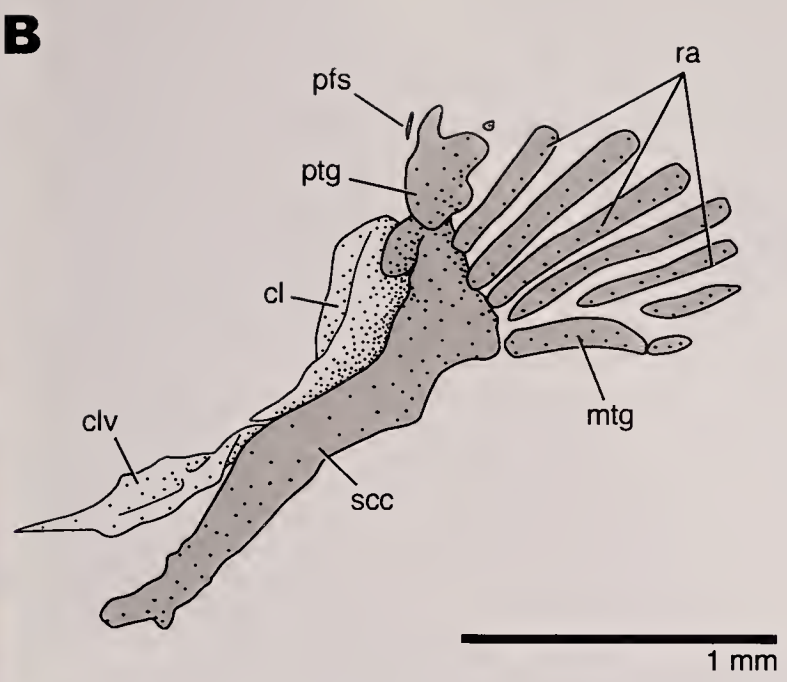
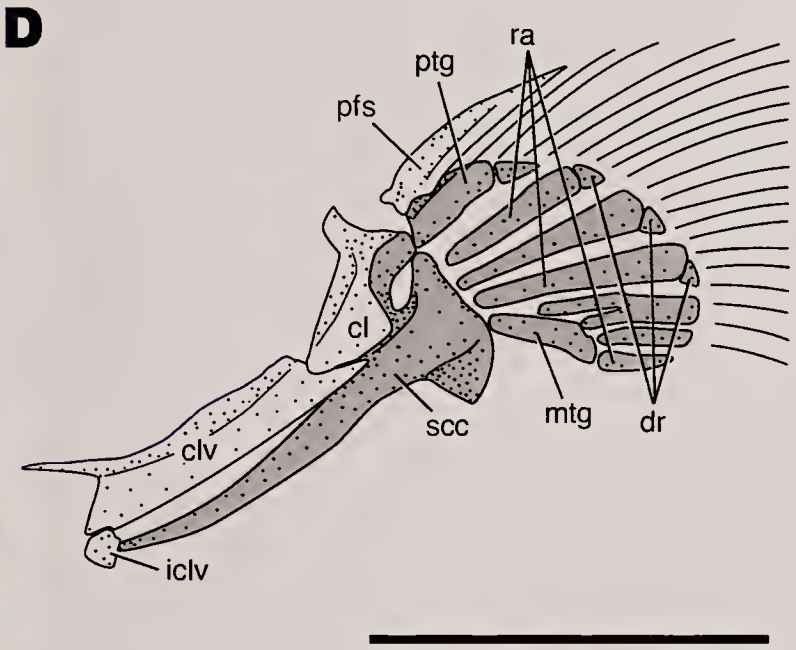
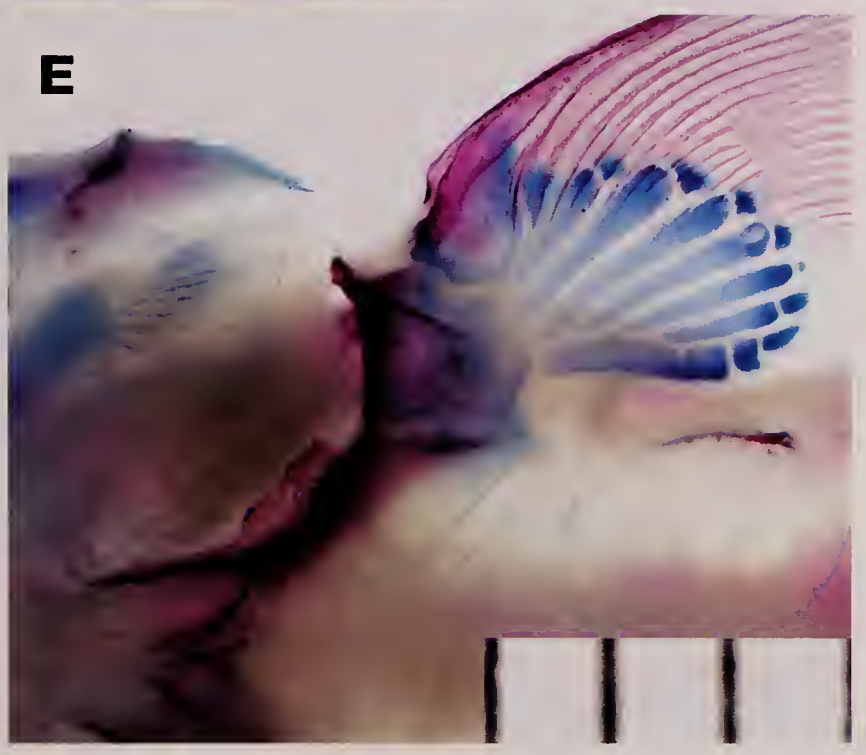


FIG. 92. *Acipenser brevirostrum*, pectoral girdle, fin supports, and fin spine in posterodorsal view, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing. In photo, bone is stained red, and cartilage appears white; in drawing, bone is white, and cartilage is gray. Anterior to left. Abbreviations found on pages 8–9.







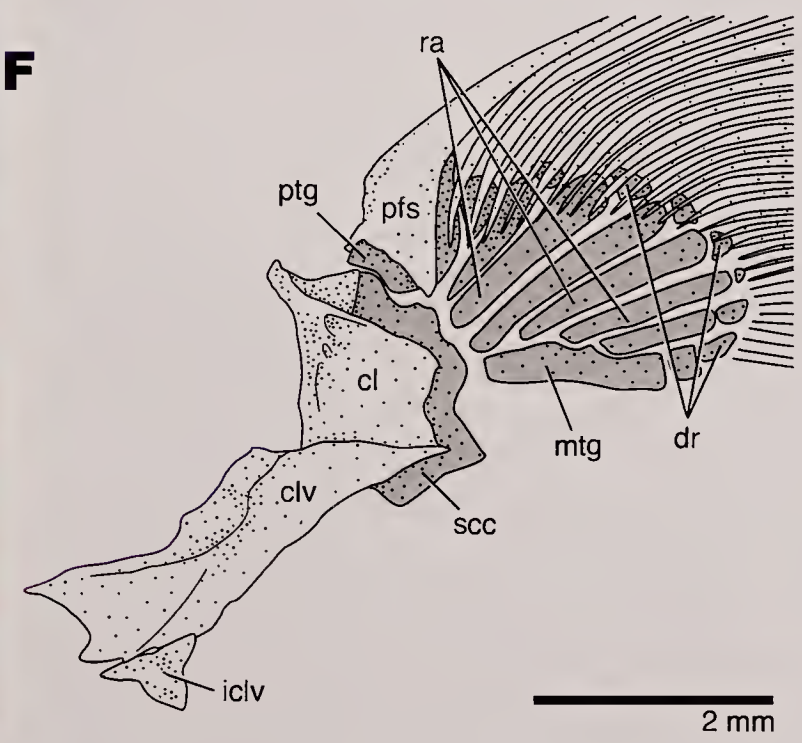
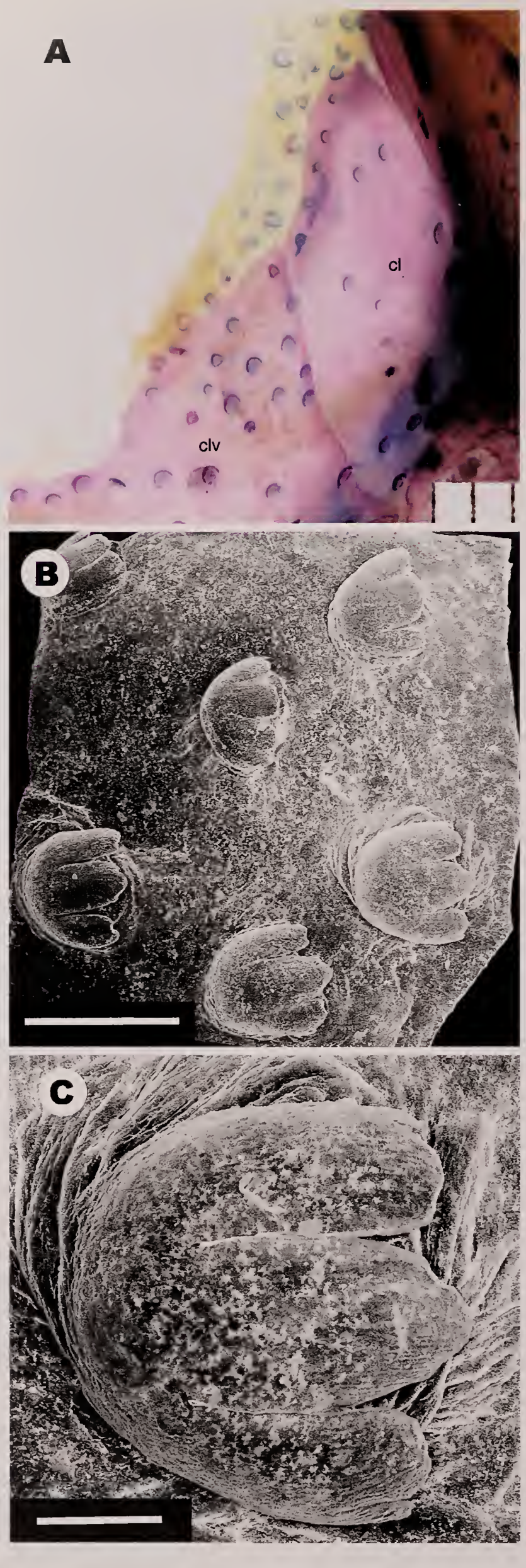


FIG. 93. *Acipenser brevirostrum*, pectoral girdle and fin at various stages of development, in ventral view. **(A, B)** VIMS 12077, 21.9 mm TL. **(C, D)** VIMS 12088, 30.5 mm TL. **(E, F)** VIMS 12081, 58.7 mm TL. Anterior to left. Abbreviations found on pages 8–9.



†*Chondrosteus*, whereas here we will discuss relationships within Acipenseridae.

Phylogenetic Analysis

Our phylogenetic analysis of the family Acipenseridae is based on characters discussed below (see also Appendix I) and the data matrix presented in Appendix II (this data matrix is virtually identical to that used by Hilton & Forey, 2009, which was completed at about the same time as the final analyses for the present study were made). As discussed by Hilton and Forey (2009), the choice is difficult for appropriate out-groups in studies of acipenseriform systematics because of the derived nature of acipenseriform anatomy (e.g., aspects of their jaw structure). Because the focus of our study is relationships among sturgeons, nonacipenserid acipenseriforms (including the polyodontids *Polyodon* and †*Protopsephurus*, the †peipiaosteid †*Peipiaosteus*, and the †chrondrosteid †*Chonodrosteus*) function as out-groups for polarization of characters within the family Acipenseridae. Further outside of Acipenseriformes, many fossil basal actinopterygian taxa are too fragmentary to be useful out-groups, and sturgeons differ so greatly from extant nonneopterygians and basal neopterygians that many of the characters used in this analysis would have to be coded as inapplicable for any taxon used as an out-group. Our use of †*Birgeria* and †*Boreosomus* as out-groups follows from the facts that †*Birgeria* has been allied to Acipenseriformes (e.g., Bemis et al., 1997) and the anatomy of †*Boreosomus* is relatively well known; we coded these taxa based on the detailed descriptions provided by Neilsen (1942, 1949, respectively).

We conducted a heuristic search using PAUP* (Swofford, 2002), using the random addition sequence option (10,000 replicates) and the tree-bisection-reconnection branch-swapping algorithm, with the starting tree obtained by stepwise addition. We used MacClade v. 4.0 (Maddison & Maddison, 2000) and Mesquite v. 1.11 (Maddison & Maddison, 2006) for our postanalytical character analysis. The two most-parsimonious cladograms (106 steps) resulting from our phylogenetic analysis of 62 characters are presented in Figure 128, and the strict consensus of the two is shown in Figure 129. Although this phylogeny must be viewed as preliminary, it does point to several aspects of sturgeon evolution that need to be examined more closely in future work (see the section Conclusions). In particular, it will be important for future studies to be based on preparation, examination, and analysis of new specimens of all sturgeon taxa not included in our analysis (and additional material of those that are treated here), including the largest specimens available to ensure that similar life history stages are being compared (i.e., adult conditions are compared to adult conditions of different taxa rather than comparisons between comparably sized individuals).

In both fundamental cladograms (Fig. 128), the position of †*Chondrosteus* is resolved as basal among Acipenseriformes,

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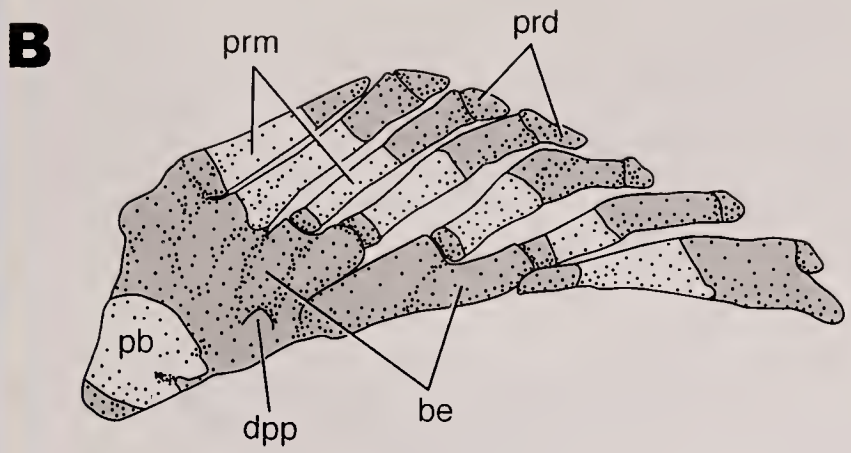
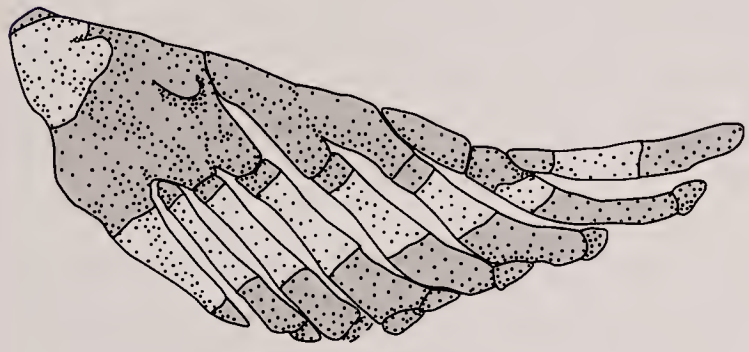
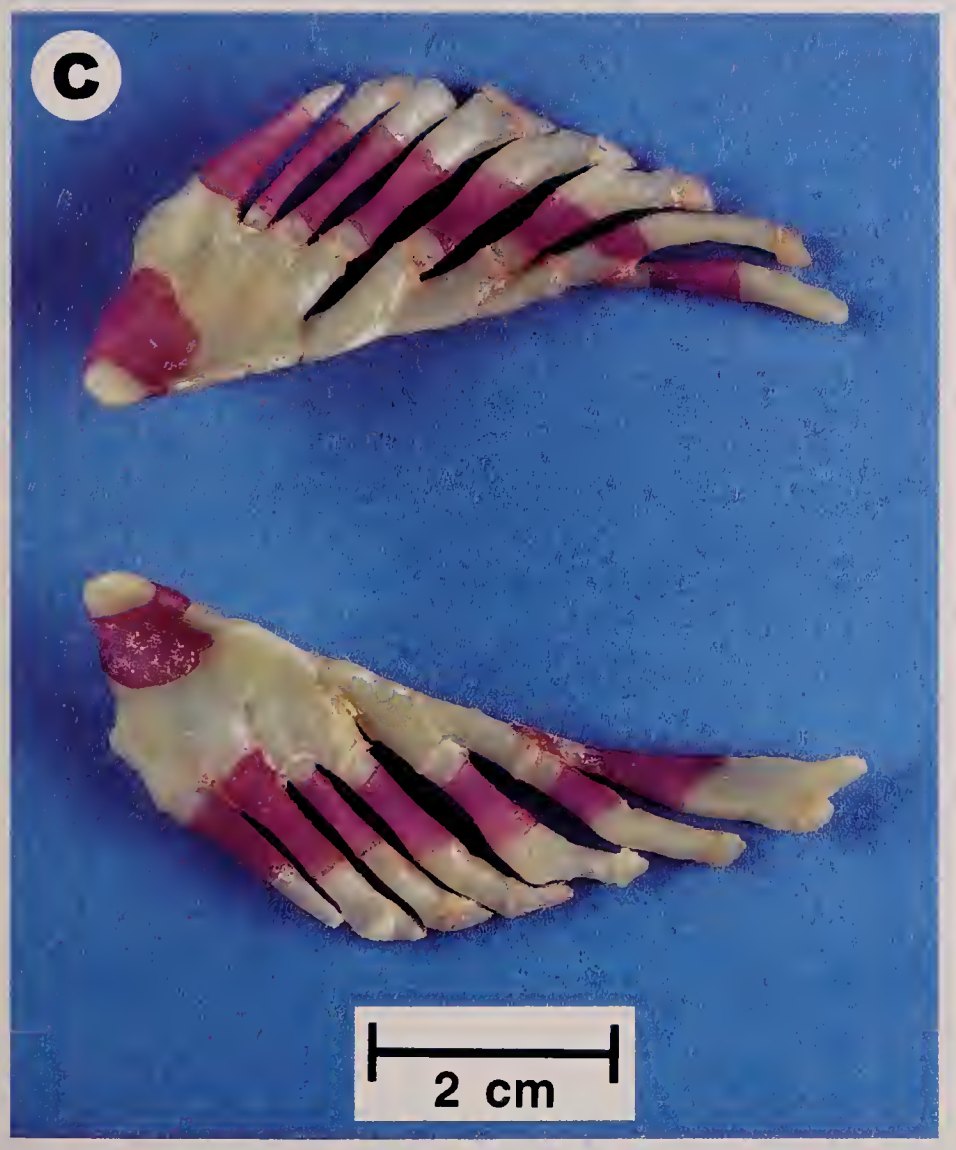
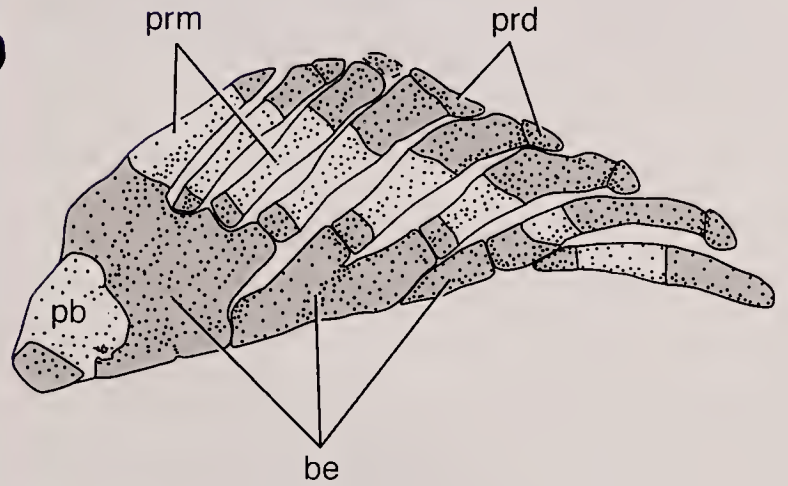
FIG. 94. *Acipenser brevirostrum*, round-based scales of the pectoral girdle. (**A**) Photo showing scattered distribution in skin covering and dorsal to the cleithrum and clavicle, from VIMS 12087 (251 mm SL). Scale bar in millimeters. Anterior to left. (**B**) Scanning electron micrograph of a small patch of skin with round-based scales from an adult (FMNH 113538, female, 960 mm SL). Scale bar = 1 mm. (**C**) Scanning electron micrograph showing an individual round-based scale (from sample shown in **B**). Scale bar = 0.25 mm. Abbreviations found on pages 8–9.









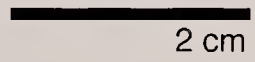
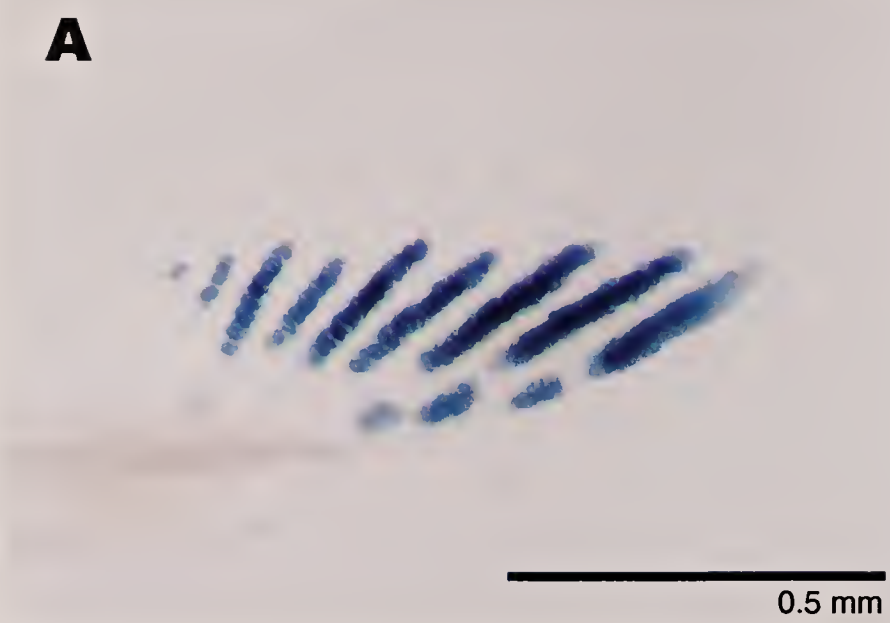
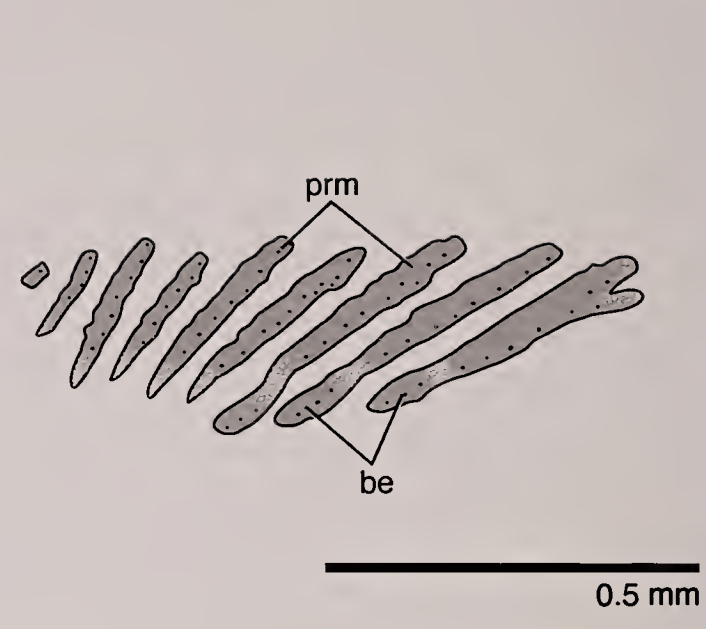
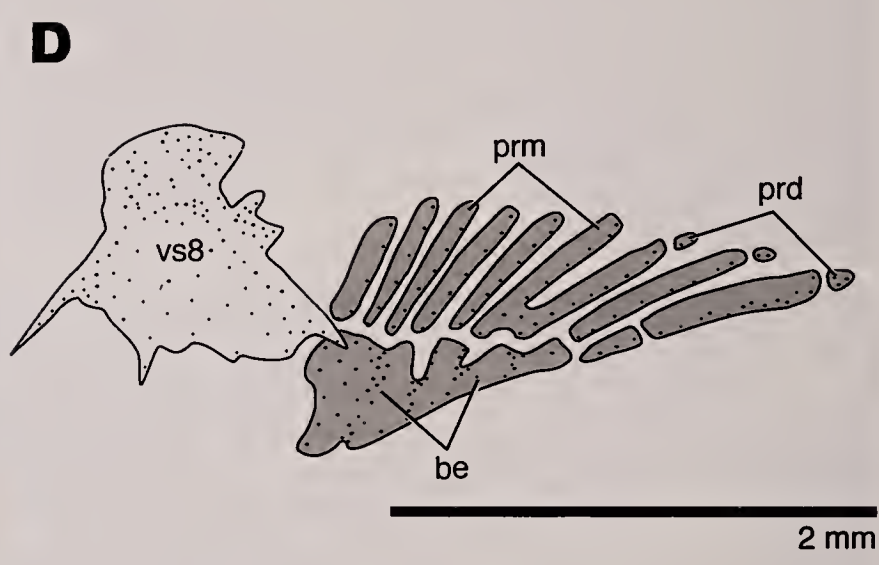
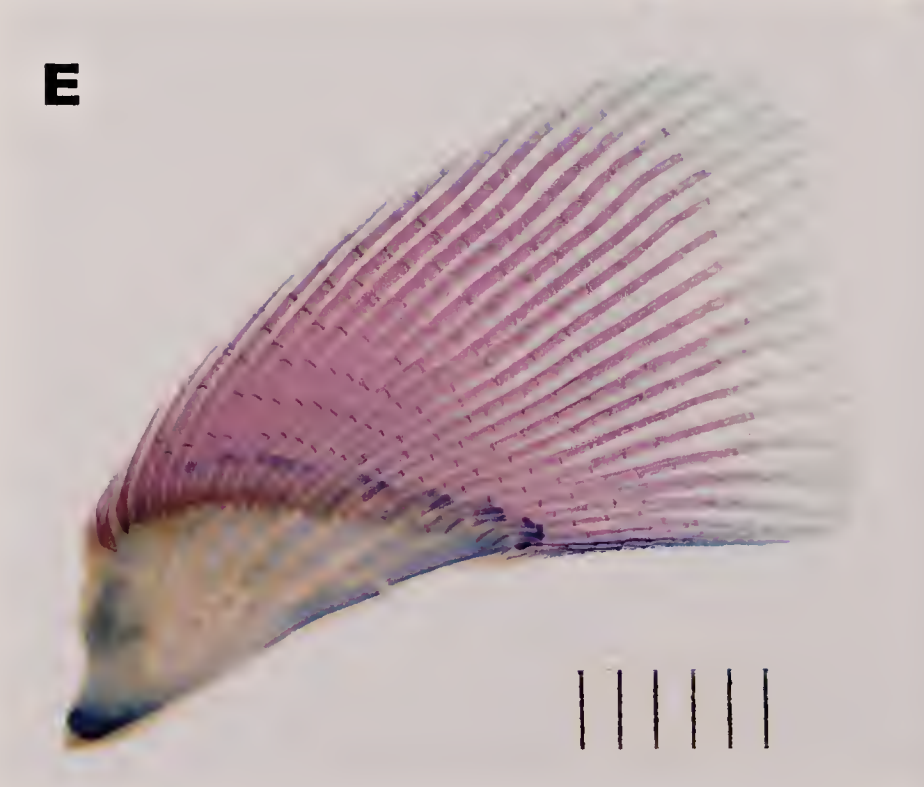


FIG. 95. *Acipenser brevirostrum*, pelvic girdle, from FMNH 113538 (female, 960 mm SL). (**A**) Photograph and (**B**) line drawing of elements in dorsal view. (**C**) Photograph and (**D**) line drawing of elements in ventral view. In photos, bone is stained red, and cartilage appears white; in drawings, bone is white, and cartilage is gray. Anterior to left. Abbreviations found on pages 8–9.









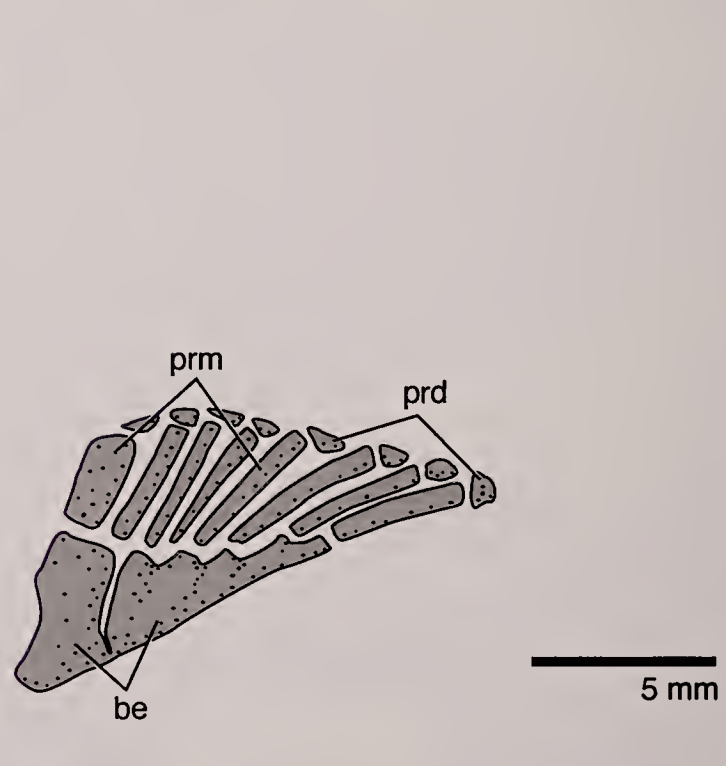


FIG. 96. *Acipenser brevirostrum*, pelvic girdle and fin at various stages of development, in ventral view. (**A, B**) VIMS 12079, 23.8 mm TL. (**C, D**) VIMS 12081, 58.7 mm TL (image reversed). (**E, F**) VIMS 12087, 251 mm SL. Anterior to left. Abbreviations found on pages 8–9.

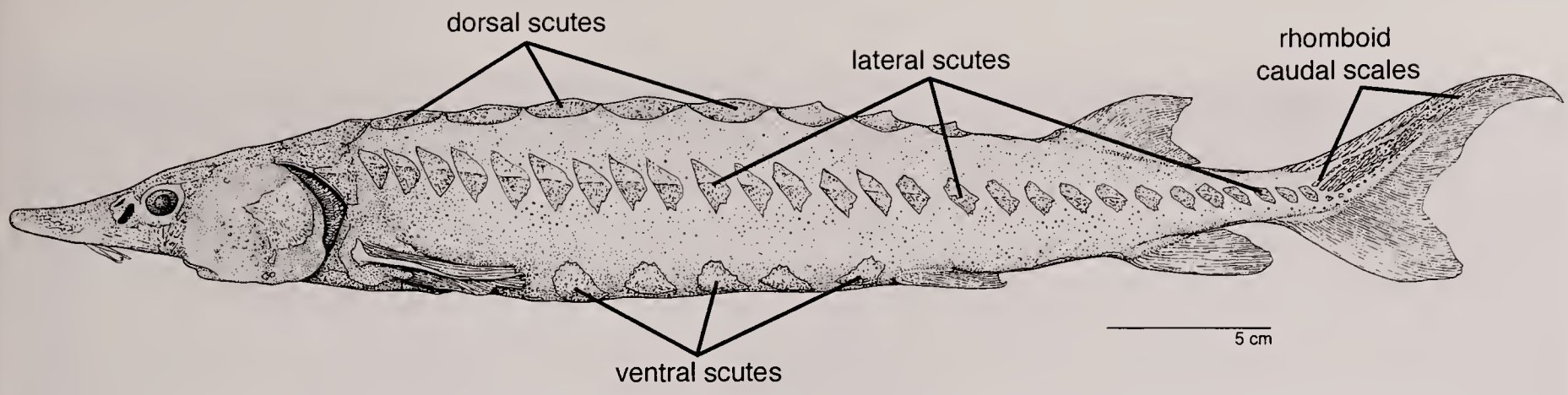


FIG. 97. *Acipenser brevirostrum*, illustration of whole specimen showing position of rows of dermal scutes and caudal scales.

relative to †*Peipiaosteus* (see Hilton & Forey, 2009, for further discussion of basal acipenseriform relationships). The topologies of the two fundamental trees differ in the relative positions of *Scaphirhynchus* and †*Priscosturion*, the clade (*A. baerii* [*H. huso*, *A. ruthenus*]), the clade (*A. stellatus* [*P. kaufmanni*, *P. hermanni*]), and the clade *A. brevirostrum* + *A. fulvescens*. †*Priscosturion* is unique within Acipenseridae, but many autapomorphic characters found in this taxon in its derived position (Fig. 128A) are reversals to the plesiomorphic state (see discussion of character transformations below). We take this, combined with its geological age, as sufficient to regard the topology shown in Figure 128B, with †*Priscosturion* the sister taxon to all other Acipenseridae, as more likely and thus is our favored topology between the two equally most-parsimonious topologies. Character support for the various nodes of the strict consensus of these two topologies is described below (see also Appendix III).

Character Support

Below we list only those characters that are resolved as uniquely derived synapomorphies in both topologies (i.e., consistency index [CI] = 1.00 in both trees), or, if there are no uniquely derived characters supporting a given node in both trees, we list those characters that are congruent between the two topologies (with CIs reported) using accelerated transformation (ACCTRAN) optimization. We favor ACCTRAN over delayed transformation because it maximizes homology statements by favoring losses of characters over their independent gains. For full character support of all nodes in both trees, see Appendix III. Where there are differences in character support for each node because of the different topologies, we discuss this in the character descriptions (see the section Character Descriptions and Discussion).

Node A (Acipenseriformes)

Palatoquadrates with symphysis between *pars autopalatina* (character 30[1])
Premaxillary and maxillary bones absent (character 32[1])

Node B (Unnamed Clade)

Branchiostegal number fewer than seven but more than one (character 24[1])
Posterior margin of the branchiostegals serrated (character 25[1])
Ossified basibranchials absent (character 40[1])
Gill rakers without teeth (character 41[1])

Node C (Acipenseroidei)

Ventral rostral bones present (character 18[1])

Node D (Polyodontidae)

Well-developed anterior and posterior divisions of the *fenestra longitudinalis* present (character 1[1])

TABLE 8. Meristic data of scutes for a growth series of *Acipenser brevirostrum*. Free dorsal scute count includes all scutes anterior to the dorsal fin except for the anteriormost scute, which becomes incorporated into skull roof.

Specimen no. (SL)	Dorsal scutes	L, R lateral scutes	L, R ventral scutes	Pre-, Postanal fin scute(s)	Postdorsal fin scute(s)
VIMS 12101 (no SL)	10	15, 18	6, 6	0, 0	0
VIMS 12082 (no SL)	10	20, 21	8, 7	1, 1	0
FMNH 112215 (50.9 mm)	11	28, 27	9, 8	2, 1	4
VIMS 12086 (71.1 mm)	11	20, 17	6, 6	1, 1	2
FMNH 112918 (80.0 mm)	10	26, 27	9, 9	1, 1	1
FMNH 112916 (85.5 mm)	9	24, 24	8, 7	1, 1	1
FMNH 112917 (104.3 mm)	11	26, 25	7, 8	1, 1	2
VIMS 12087 (251 mm)	11	24, 24	7, 8	1, 1	1
MCZ 54167 (472 mm)	12	29, 29	8, 8	1, 1	1
FMNH 117461 (640 mm)	9	28, 29	8, 7	3, 1	1
ANSP 16953 (690 mm)	11	26, 28	?, ?	2, 1	1
FMNH 112212 (710 mm)	11	34, ?*	8, 9	4, 1	3
FMNH 112913 (755 mm)	10	28, ?*	9, 7	1, 1	2
UMA F10578 (899 mm)	11	29, ?*	9, ?*	2, 2	2
FMNH 113538 (960 mm)	11	30, 30	10, 11	3, 1	3

* Only left side counted before dissection.

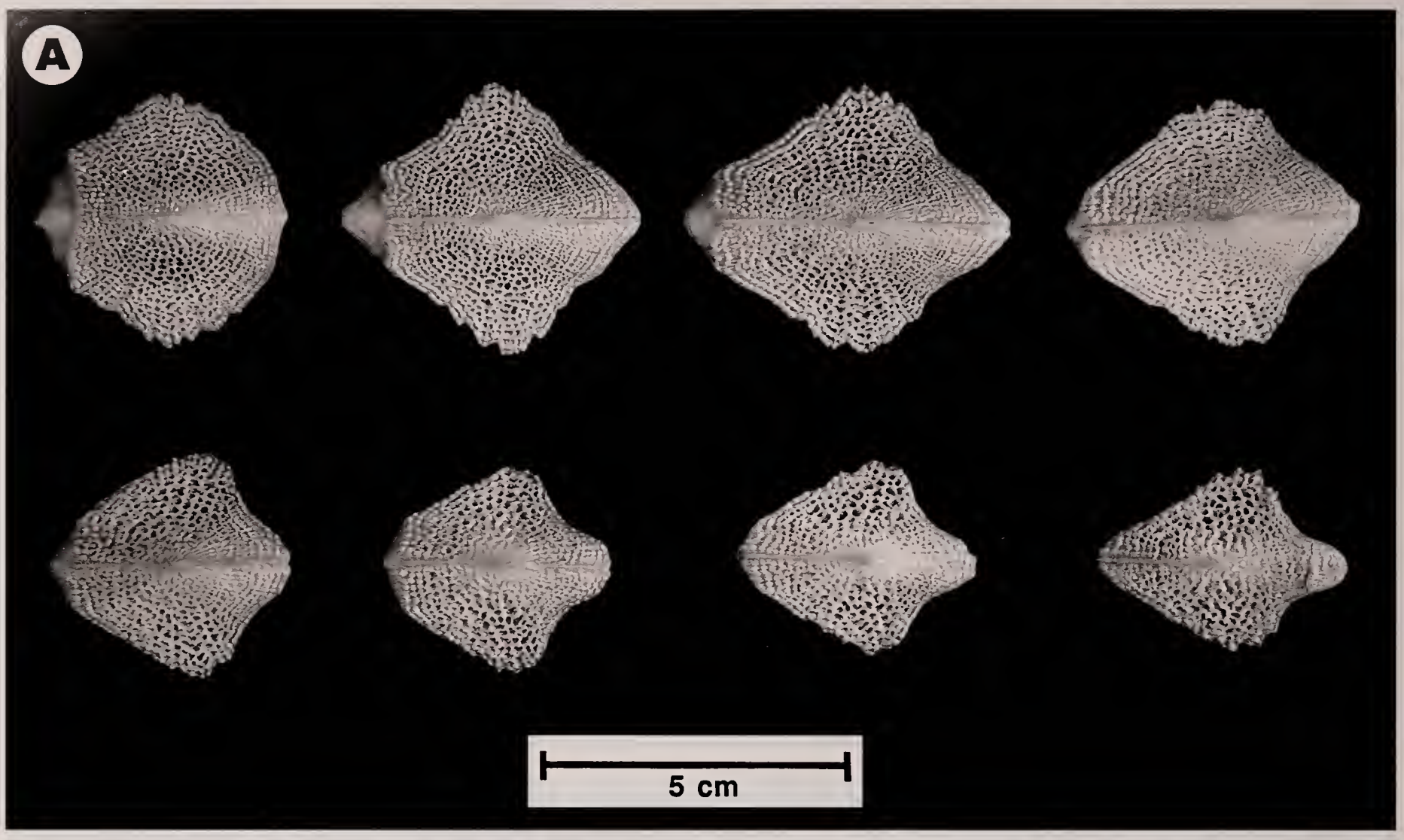


FIG. 98. *Acipenser brevirostrum*, dorsal scutes in dorsal view, from FMNH 112214 (sex unknown, 763 mm SL). (**A**) Photograph and (**B**) line drawing. Anterior to left.

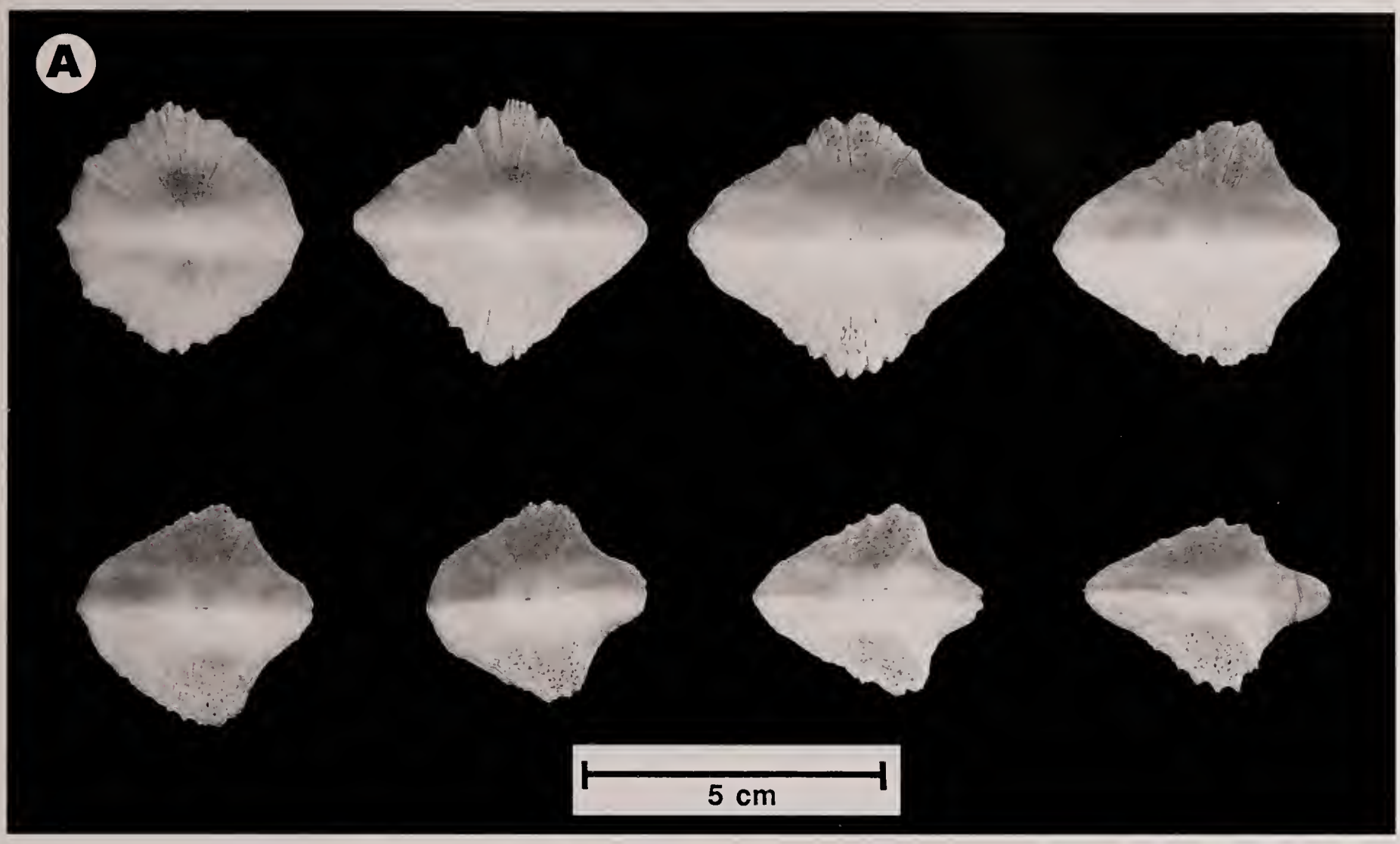


FIG. 99. *Acipenser brevirostrum*, dorsal scutes in ventral view, from FMNH 112214 (sex unknown, 763 mm SL). (**A**) Photograph and (**B**) line drawing. Anterior to left.

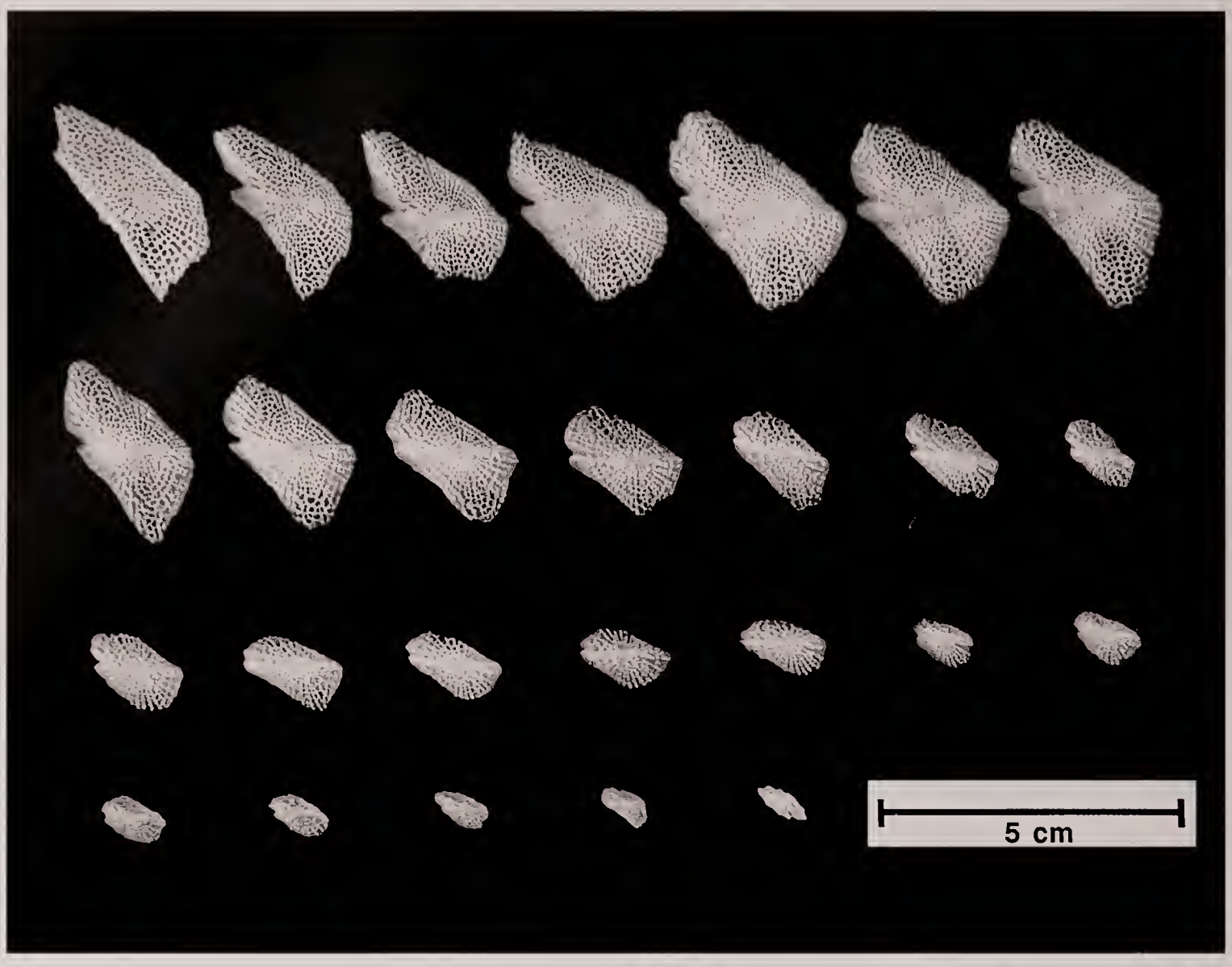


FIG. 100. *Acipenser brevirostrum*, lateral scutes in lateral view, from FMNH 112214 (sex unknown, 763 mm SL). Anterior to left.

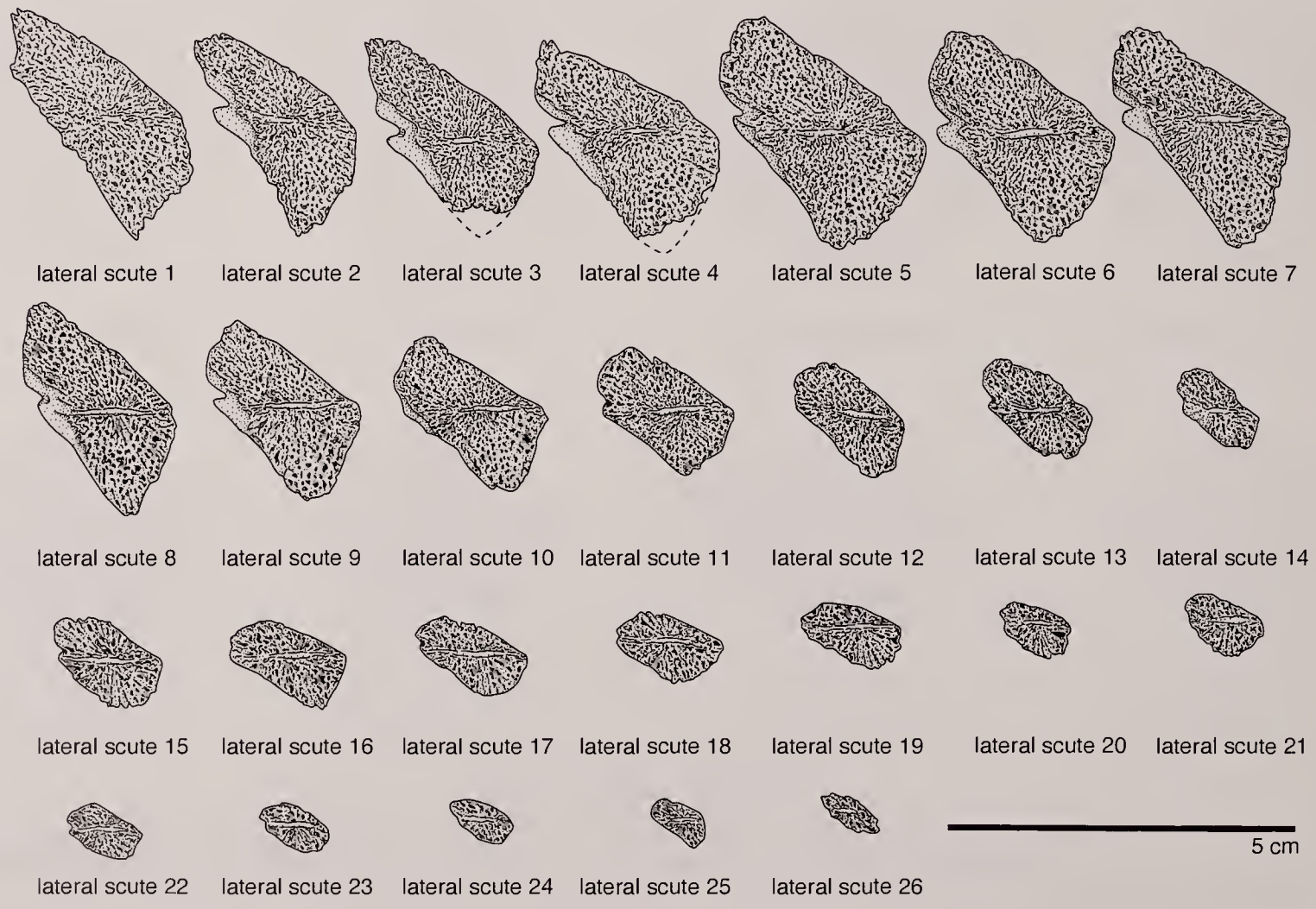


FIG. 101. *Acipenser brevirostrum*, lateral scutes in lateral view, from FMNH 112214 (sex unknown, 763 mm SL). Line drawing of Figure 100. Anterior to left.

FIG. 102. *Acipenser brevirostrum*, lateral scutes in medial view, from FMNH 112214 (sex unknown, 763 mm SL). Anterior to left (images reversed to show medial surface of elements but with anterior to left).

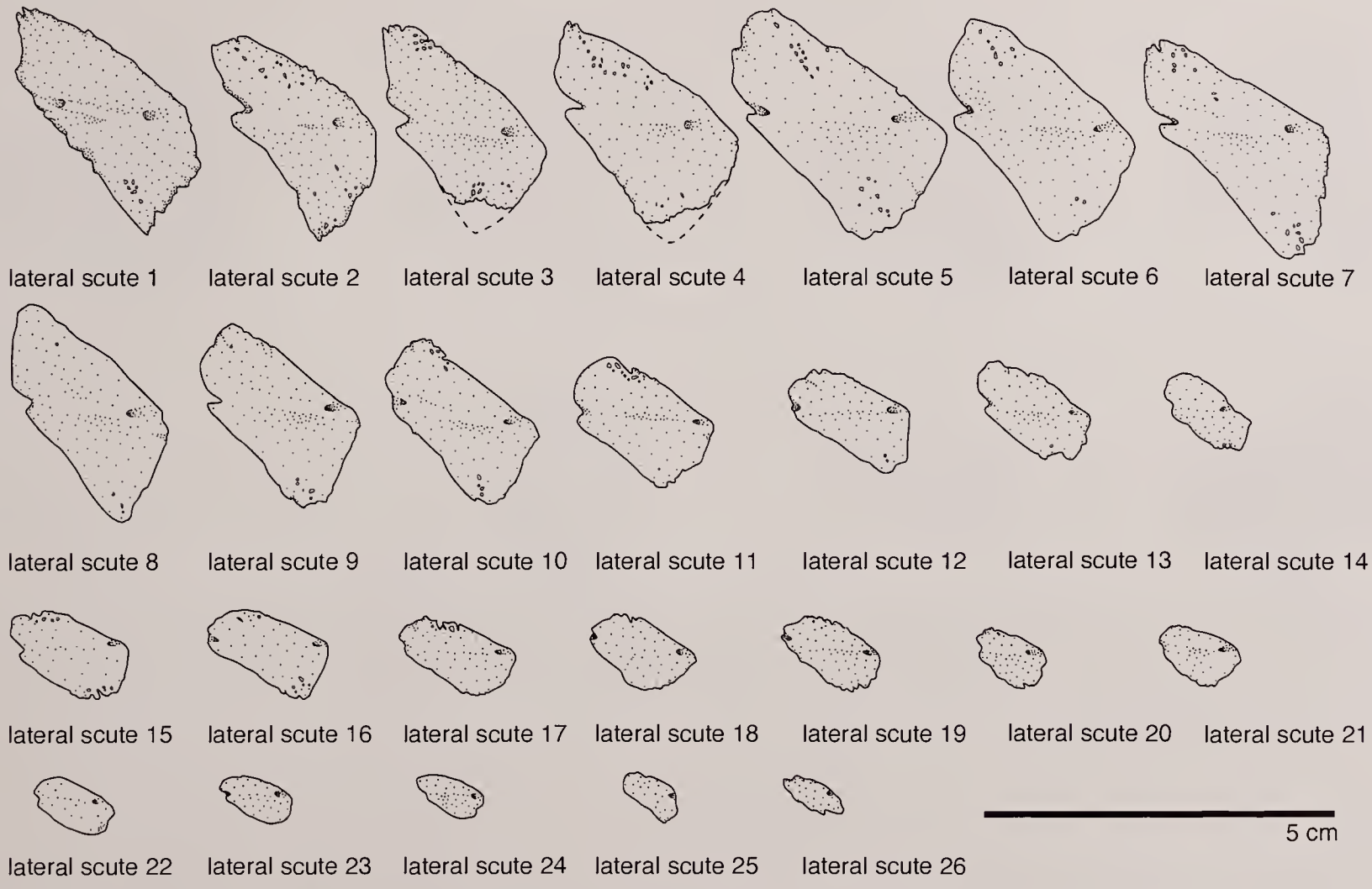


FIG. 103. *Acipenser brevirostrum*, lateral scutes in medial view, from FMNH 112214 (sex unknown, 763 mm SL). Line drawing of Figure 102. Anterior to left.

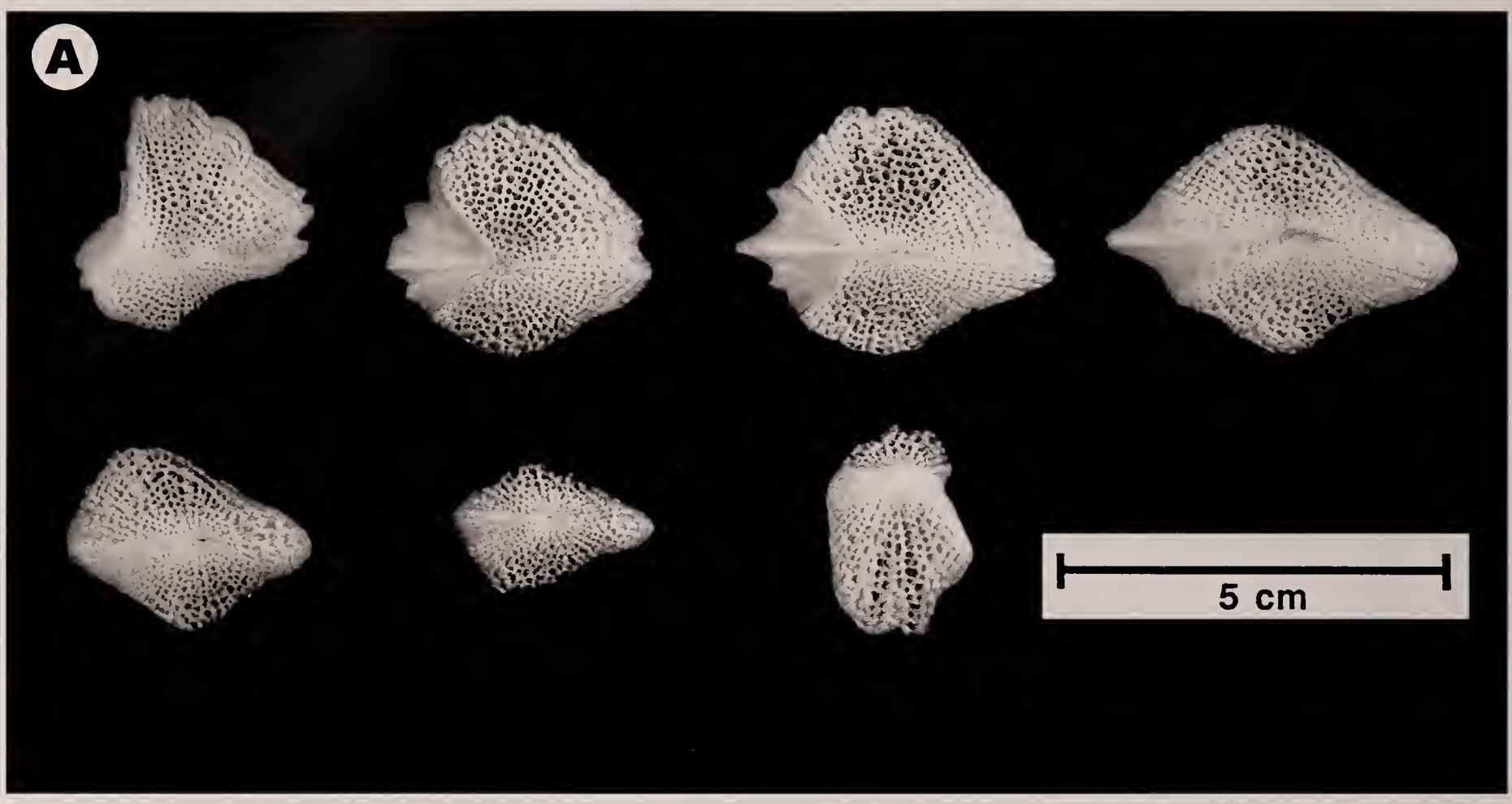


FIG. 104. *Acipenser brevirostrum*, ventral scutes in lateral view, from FMNH 112214 (sex unknown, 763 mm SL). (**A**) Photograph and (**B**) line drawing. Anterior to left.

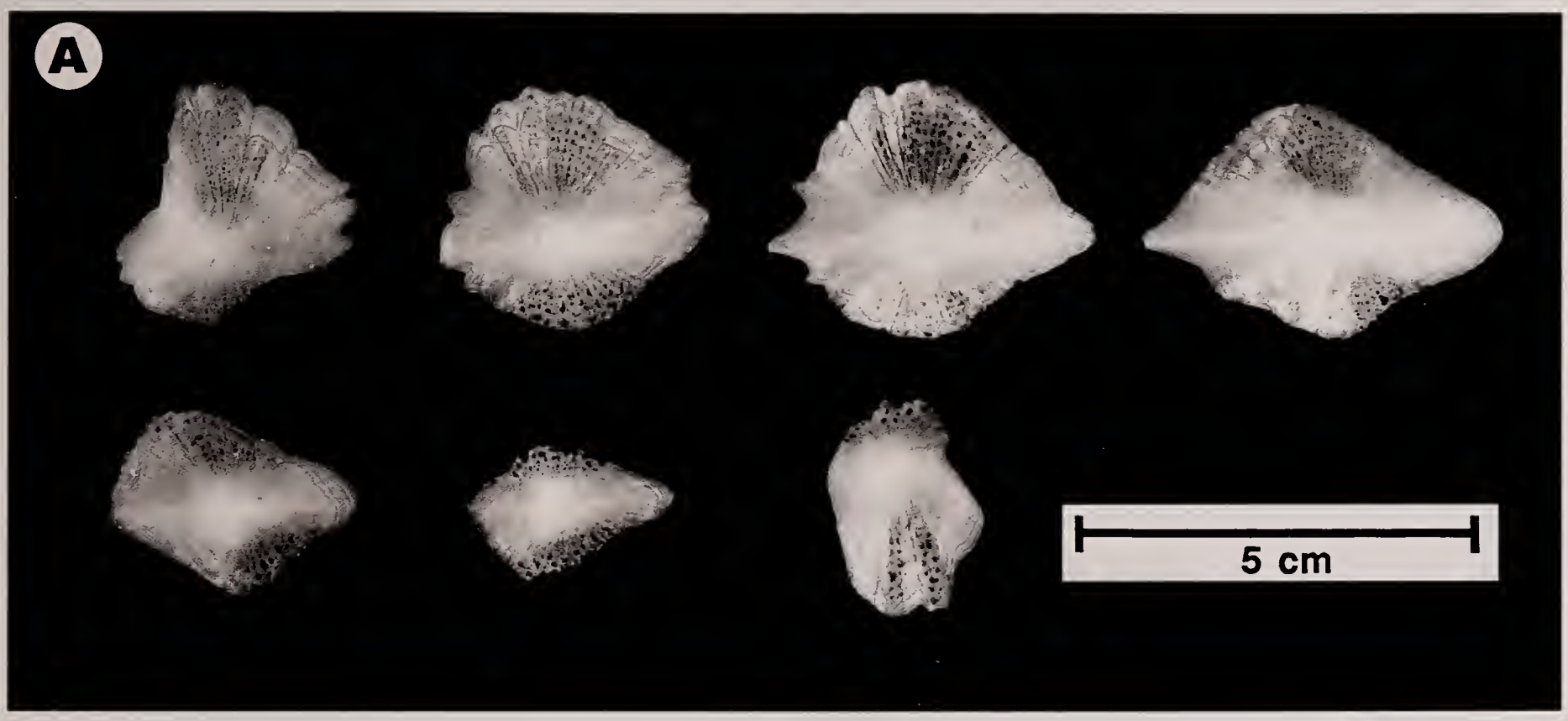


FIG. 105. *Acipenser brevirostrum*, ventral scutes in medial view, from FMNH 112214 (sex unknown, 763 mm SL). (**A**) Photograph and (**B**) line drawing. Anterior to left (images reversed to show medial surface of elements but with anterior to left).

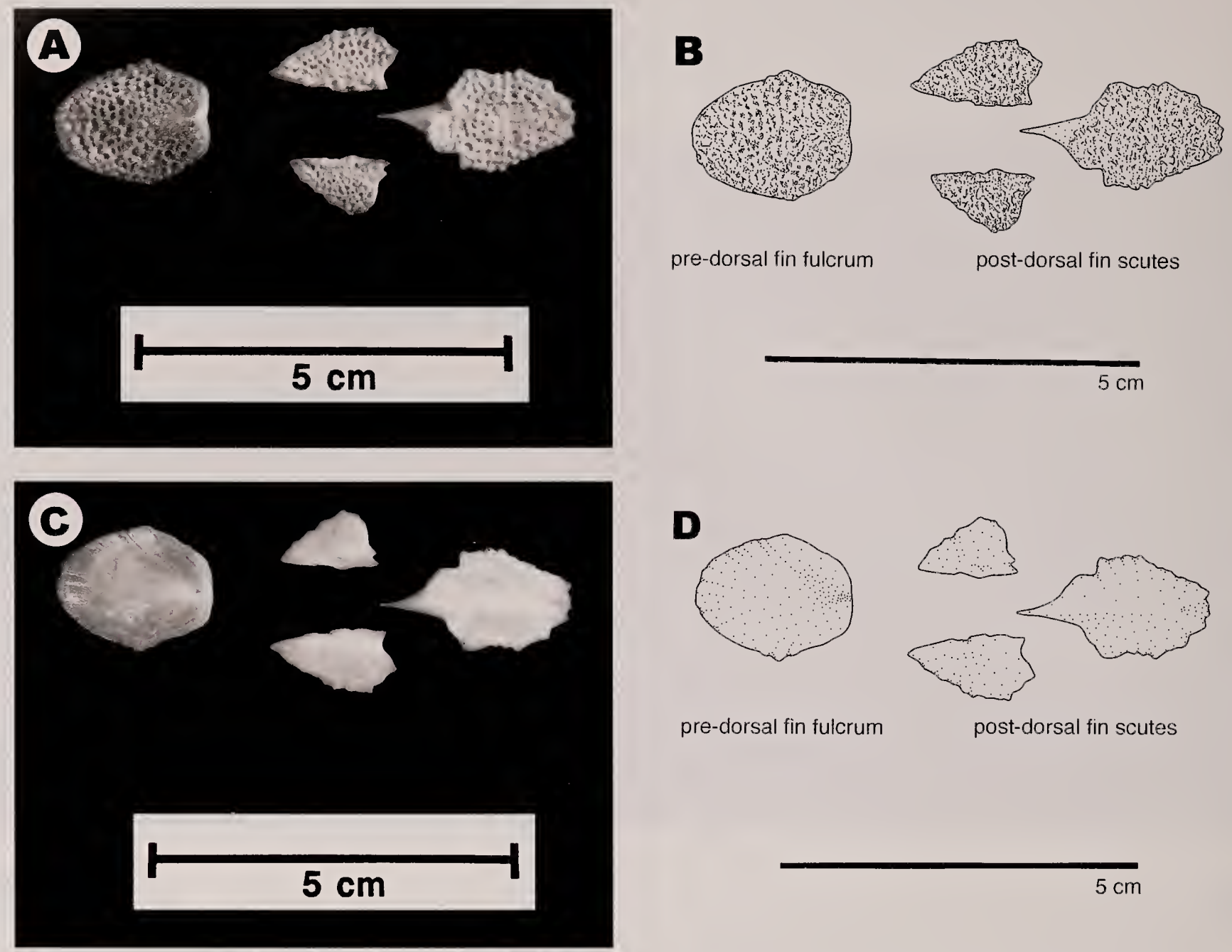


FIG. 106. *Acipenser brevirostrum*, predorsal fin fulcrum and postdorsal fin scutes, from FMNH 112214 (sex unknown, 763 mm SL). (**A**) Photograph and (**B**) line drawing of elements in dorsal view. (**C**) Photograph and (**D**) line drawing of elements in ventral view. Anterior to left.

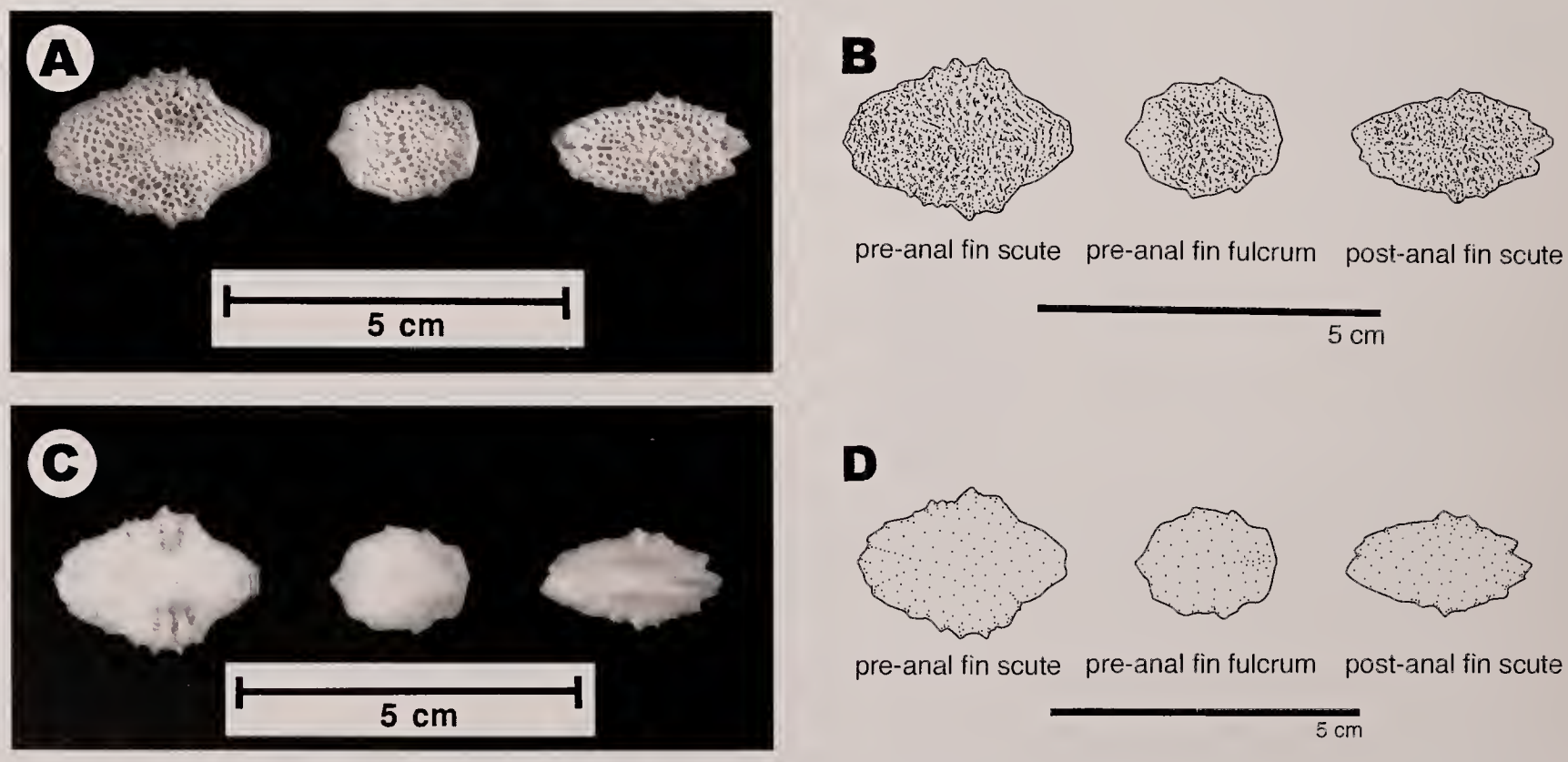


FIG. 107. *Acipenser brevirostrum*, preanal fin scute, preanal fin fulcrum and postanal fin scute, from FMNH 112214 (sex unknown, 763 mm SL). (**A**) Photograph and (**B**) line drawing of elements in dorsal view. (**C**) Photograph and (**D**) line drawing of elements in ventral view. Anterior to left.

Parietals extending posterior to posttemporals (character 3[1])
Stellate bones present (character 4[1])
Posterior margin of subopercle serrated (character 28[1])
"Microctenoid" scales present (character 43[1])

Node E (Acipenseridae)

Rostral canal curves (character 11[1])
Posteriormost ventral rostral bone single (character 19[1])
Branchiostegals of different shapes (character 23[1])
Dorsalmost branchiostegal pillar-like and laterally concave (character 26[1])
Palatal complex present (character 29[1])
Anterior shelf of hypobranchial one present (character 38[1]
Continuous series of median dorsal scutes extending from skull to dorsal fin present (character 45[1])
Supracleithrum reaching level of extrascapulars (character 54[1])
Cardiac shield formed by shoulder girdle present (character 56[1])
Clavicle and cleithrum suture present, tight and interdigitating (character 58[1])
Supracleithral cartilage present (character 59[1])

Node F (Unnamed Clade)

Ventral rostral bones with a variable number of distinctly raised prominences (character 21[1])

Node G (Husinae, new usage)

Frontal bones meet in midline (character 2[1], CI = 0.25)
Medial dermopalatine expansion with a slight medial broadening (character 34[1], CI = 0.67)

Node H (Pseudoscaphirynchinae, new subfamily)

Horizontal arm of jugal bone undercuts nasal capsule (character 7[1])

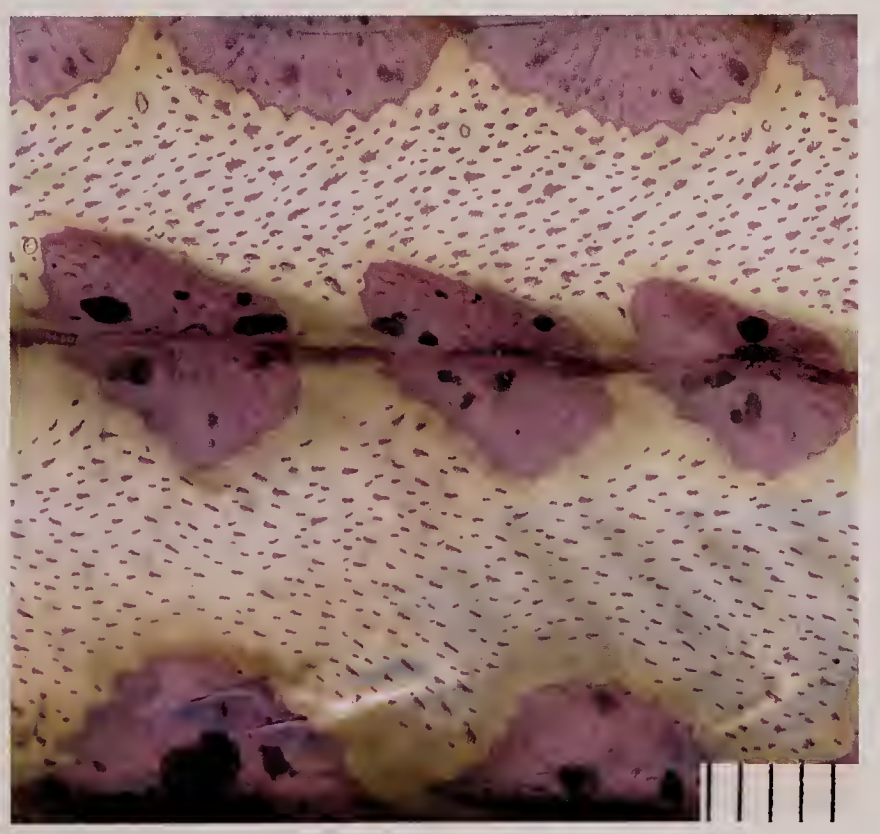


FIG. 108. *Acipenser brevirostrum*, section of cleared and stained skin showing a portion of lateral scutes and the dermal ossicles found between scute rows, from VIMS 12087 (251 mm SL). Note also the tubular ossifications of the lateral line sensory canals between adjacent lateral scutes. Scale in millimeters. Anterior to left.

*Node I (*Pseudoscaphirhynchus*)*

Caudal peduncle scutes arranged as lateral, paired dorsal, large scutes intercalated between lateral series and ventral midline but not organized in distinct series (character 50[3])

Node J (Unnamed Clade)

Jugal bone with horizontal and vertical arms not distinct (triangular) (character 5[1]; CI = 0.50).

Character Descriptions and Discussion

In this section, we discuss the characters used in our phylogenetic analysis. For ease of comparison with our illustrations, the characters are listed according to anatomical region or complex.

Character 1. Well-developed anterior and posterior divisions of the fenestra longitudinalis (0 = absent; 1 = present).

The *fenestra longitudinalis* is an opening on the lateral portion of the skull roof, and in polyodontids, there is an anterior *fenestra longitudinalis* (defined by the frontal, dorsal rostral bones, dermosphenotic, and the intertemporal–supratemporal) and a posterior *fenestra longitudinalis* (defined by the intertemporal–supratemporal, frontal, parietal, and the posttemporal). This character was found to be a synapomorphy of Polyodontidae by Grande and Bemis (1991, character 18), as it was in our analysis (see also Grande & Hilton, 2006, character 8).

Character 2. Contact at midline between frontal bones (0 = absent; 1 = present).

The left and right frontal bones of sturgeons may be either in contact with one another or separated from one another, typically by a series of dorsal rostral bones. Having the frontals separated in the midline is considered plesiomorphic for Acipenseridae (found also in †*Peipiaosteus* and †*Protopsephurus*, although the frontals meet in the midline of *Polyodon* and *Psephurus*). Having the left and right frontals contact each other in the midline was found to support *A. ruthenus* + *Huso* and is independently derived in *A. oxyrinchus*. Within some acipenserid taxa, there is slight variation, although a typical condition can be reliably identified. For example, in *A. brevirostrum*, only two individuals of the more than 50 large specimens examined here were found to have the left and right frontals in contact in the midline. This is in contrast to taxa such as *A. oxyrinchus* in which all specimens examined had the frontals in contact in the midline (Fig. 131B). This character was coded as polymorphic for *A. ruthenus* following conditions seen on available specimens and those illustrated by Kittary (1850; Fig. 131E), Sewertzoff (1926c), and Marinelli and Strenger (1973). *Huso* was coded based on the illustration in Kittary (1850; Fig. 130D), a presumed adult, because the available specimens in this study are too small to confidently score this character (i.e., the skull roofing bones are not fully formed).

This character, in some ways, is related to Findeis's (1997, character 32) character of the presence and absence of "pineal" bones. Findeis (1997) considered the presence of so-called pineal bones to be a synapomorphy of all sturgeons

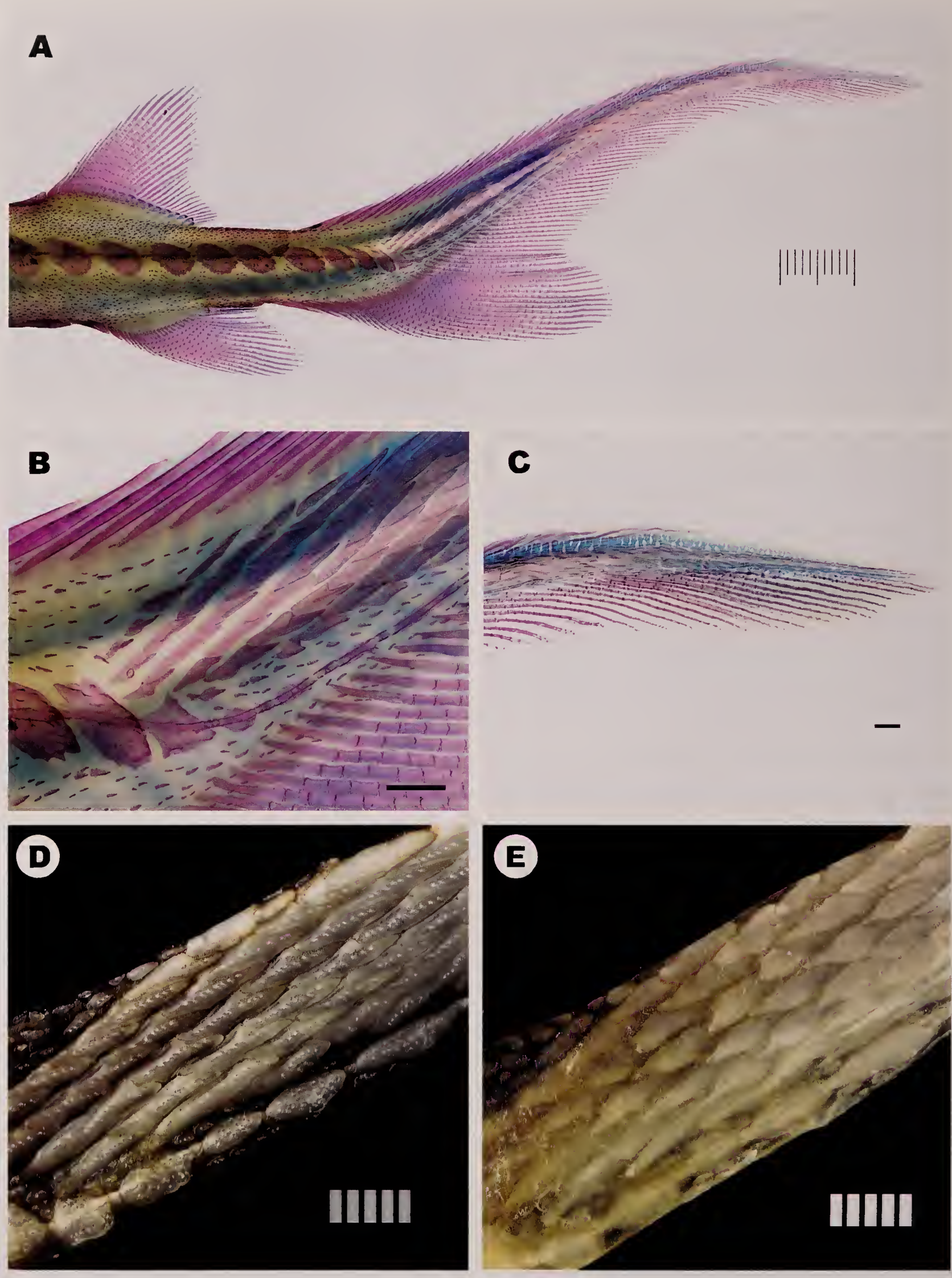


FIG. 109. *Acipenser brevirostrum*, scales of caudal region. (**A**) Caudal peduncle region. (**B**) Close-up showing dorsal bend of lateral line canal at base of caudal fin and anterior rhombic caudal scales. (**C**) Tip of tail showing posterior tip of lateral line and posterior dorsal caudal fulcra. (**D**) External and (**E**) internal views of a patch of rhombic caudal scales and posterior ossifications of the lateral line from an adult specimen (image in **E** reversed). **A–C**, VIMS 12087 (251 mm SL); (**D, E**) FMNH 112212 (sex unknown, 710 mm SL). (**A, D, E**) Scale in millimeters. (**B, C**) Scale = 2 mm. Anterior to left.

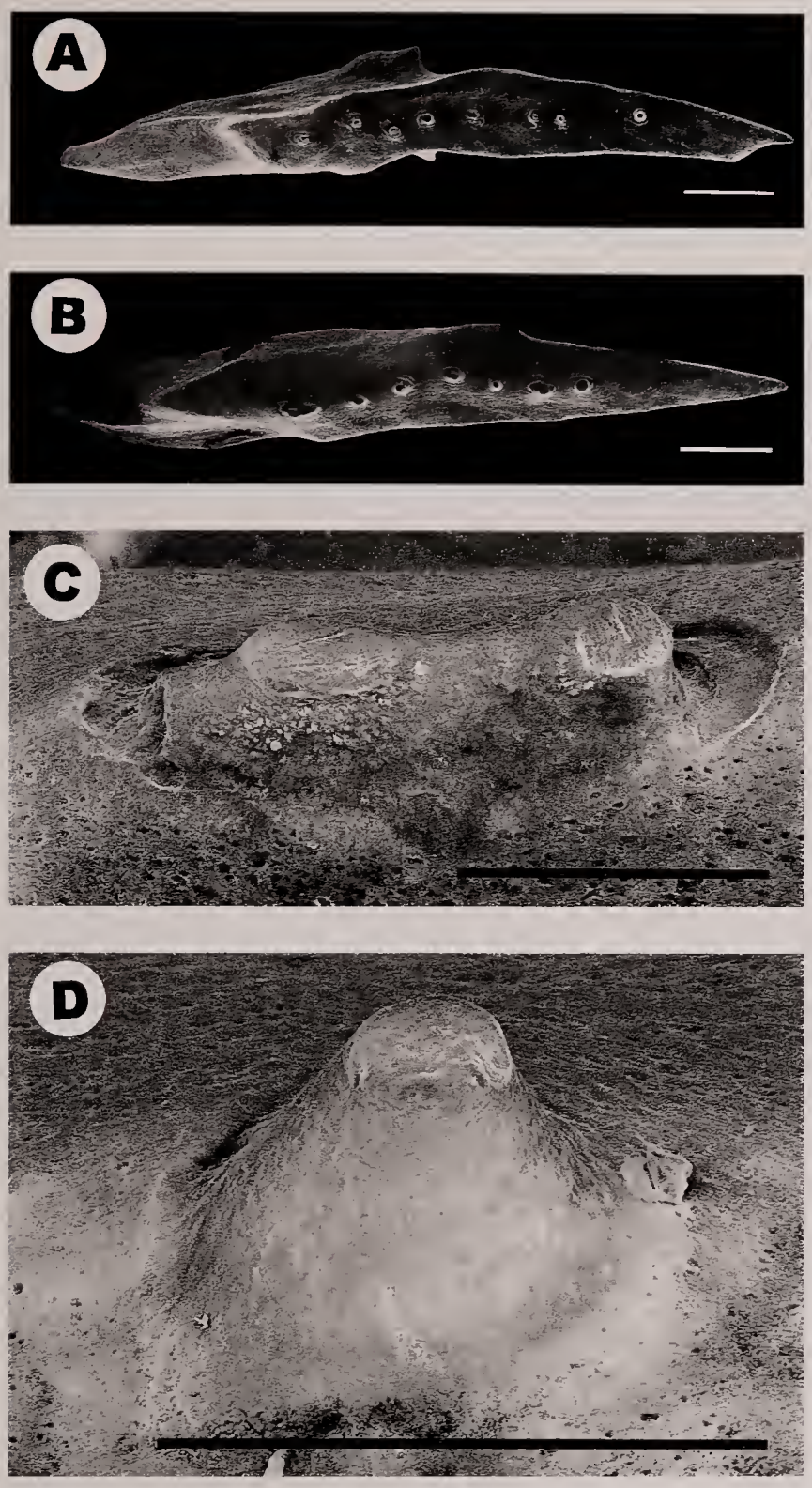


FIG. 110. *Acipenser brevirostrum*, rhombic caudal scales and denticles. (**A, B**) Scanning electron micrographs of isolated rhombic caudal scales, from FMNH 112915 (sex unknown, 605 mm SL). Scale = 1 mm. Anterior to left. Note overlapped portion exposed along anterior and dorsal margins. (**C, D**) SEM close-ups of denticles on scale shown in **B**; scale = 0.25 mm. **C** showing two denticles fused at bases. Note that tips of denticles shown in both **C** and **D** have been broken.

except *Huso*. However, his pineal bones are a portion of the anamestic series of dorsal rostral bones that are positioned between the anterior portions of the frontals. We, however, do not consider these bones a discrete series of elements and are highly variable in their form, number, and position.

Character 3. Posterior extent of parietals (0 = ending anterior to posttemporals; 1 = extending posterior to posttemporals).

Having the posterior tips of the parietals extend posterior to the posterior edge of the posttemporals is found only in Polyodontidae (see Grande et al., 2002, character 32). Acipenseridae do have elongate posterior extensions of the parietals, but they reach only the level of the midpoint of the posttemporals.

Character 4. Stellate bones (0 = absent; 1 = present).

Stellate bones are small, irregularly shaped bones that form much of the snout of paddlefishes. This character was found to be a synapomorphy of Polyodontidae by Grande and Bemis (1991, character 15), as it was in our analysis (see also Grande & Hilton, 2006, character 9). The number of stellate bones varies within Polyodontidae, ranging from few elements (e.g., †*Protopsephurus* and *Psephurus*) to very numerous (e.g., *Polyodon* and †*Crossopholis*, in which they form a dense meshwork supporting the paddle-like rostrum). Stellate bones are not found outside of Polyodontidae, although based on position (i.e., lateral to the dorsal ventral rostral bones), they may bear some correspondence to the border rostral bones of Acipenseridae.

Character 5. Shape of jugal bone (0 = distinct horizontal and vertical arms [reverse-L shaped]; 1 = horizontal and vertical arms not distinct [triangular]).

The jugal bone in Acipenseriformes, if present (the jugal is absent as a distinct element in †*Peipiaosteus* and polyodontids and therefore is coded as missing because of uncertain homology; i.e., a chain of bones is present, but one individual bone cannot be singled out as a jugal), is composed of horizontal and vertical arms. In *A. brevirostrum* and *A. fulvescens*, among the taxa studied, the space anterior to the vertical arm and dorsal to the horizontal arm becomes filled in with bone during ontogeny so that in lateral view the jugal of the adult is triangular in outline (definition of this character follows the observations of Hilton, 2002a); this is considered a synapomorphy of these taxa. The derived state is only otherwise found in †*Birgeria*, which is considered to be an independent occurrence.

Character 6. Postorbital bone (0 = present; 1 = absent).

The series of bones associated with the infraorbital sensory canal of Acipenseriformes posterior to the orbit typically comprises two bones: a dorsal postorbital and a ventral jugal. †*Chondrosteus* is the only acipenseriform that lacks a postorbital. This character is coded as "?" in †*Priscosturion* because of a lack of preservation of any bones posterior to the orbit and in †*Peipiaostens*, *Polyodon*, and †*Protopsephurus* because of unclear homology, as there is a chain of small ossicles, none of which can be homologized specifically with the jugal or postorbital.

Character 7. Anterior extent of horizontal arm of jugal bone (0 = does not reach nasal capsule; 1 = undercuts nasal capsule).

In acipenserids, the anterior tip of the horizontal arm of the jugal generally lies under the orbit. Findeis (1997, character 57) defined this character and considered it a synapomorphy of the genus *Pseudoscaphirhynchus*. In *Psendoscaphirhynchus*, the horizontal arm of the jugal is greatly expanded and reaches a point of the skull under the nasal capsule. This condition is otherwise seen only in *A. stellatus* and was found in our analysis to be a synapomorphy of *A. stellatus* + *Pseudoscaphirhynchus*. This character needs further study, as some specimens of *A. daybryanus*, for instance, also show an anteriorly extended horizontal arm of the jugal, so it may be a character at a higher level of generality (*A. dabryanus* was

FIG. 111. †*Priscosturion longipinnis* (MOR 1184, est. 800 mm TL) in (**A**) dorsal and (**B**) lateral views. Anterior to left. (**C**) oblique dorsolateral view. Anterior to bottom left of photo.

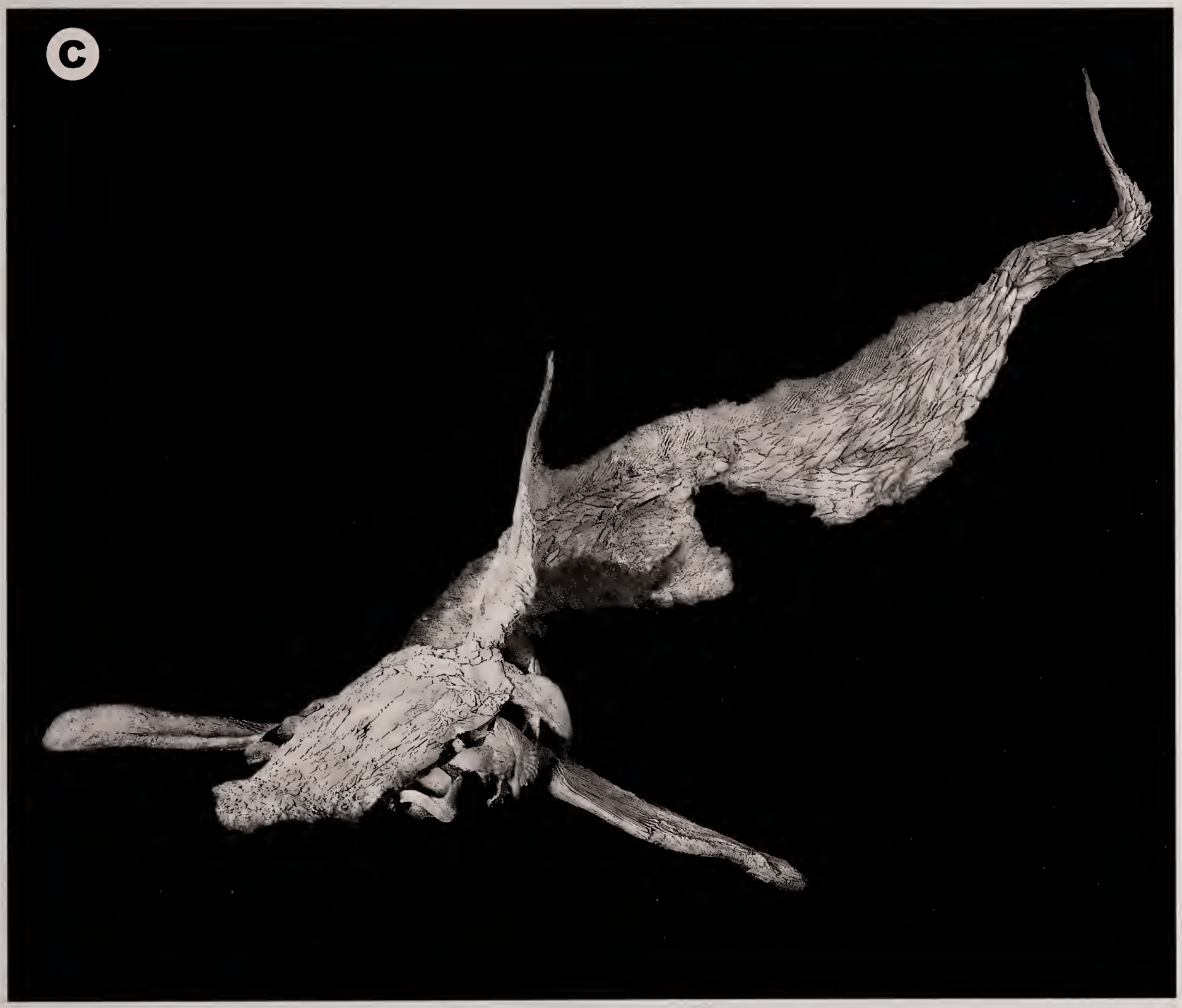


FIG. 111. *Continued.*

FIG. 112. Whole specimens of (**A**) *Acipenser brevirostrum* (MCZ 54265; 405 mm SL) and (**B**) *Huso huso* (MCZ 54269, 228 mm SL) in dorsal view. Anterior to left.

not included in our analysis because of insufficient material available).

Character 8. Medial process of jugal (0 = present; 1 = absent).

As for character 7, Findeis (1997, character 57), in describing the form of the jugal in acipenserids, considered the absence of a distinct median process on the jugal to be a synapomorphy of the genus *Pseudoscaphirhynchus*. In this genus, the medial margin of the jugal is smoothly curved in ventral view; a similar condition is found in *A. stellatus* (see Hilton, 2005). This character is coded as absent in out-groups (Nielsen, 1942, 1949) and †*Chondrosteus* (the condition in †*Chondrosteus* was seen only in a single disarticulated specimen in the possession of Mr. Chris Moore of Charmouth, England; Hilton & Forey, unpubl.), as unknown in †*Priscosturion* because of lack of preservation, and as unknown in †*Peipiaosteus* and polyodontids because of unknown homology. In one of the two fundamental cladograms (Fig. 128B), this character is recovered as a synapomorphy for *A. stellatus* + *Pseudoscaphirhynchus*. In the other cladogram (Fig. 128A), the presence of a median process is considered a synapomorphy of all acipenserids except *A. stellatus* + *Pseudoscaphirhynchus*, although this is due to optimization of question marks in polyodontids and †*Peipiaosteus*.

Character 9. Supraorbital bone (0 = absent; 1 = present without a descending process; 2 = present with a wedge-shaped descending process; 3 = present with a greatly expanded descending process).

The form of the supraorbital bone in Acipenseridae is variable, and Findeis (1997, characters 4 and 46) defined two characters related to its shape, which we have combined into this one multistate character. Basal acipenseriforms (†*Chondrosteus* and †*Peipiaosteus*) and polyodontids lack a supraorbital bone (present in out-groups) and are therefore coded as 0. Within Acipenseridae, †*Priscosturion* has a flat dermal skull roofing element identified by Grande and Hilton (2006) as a supraorbital bone. In extant sturgeons, there are distinct descending processes from the anterior portion of the supraorbital that defines the anterior extent of the bony orbit (although this process is deeply covered with soft tissue, and the eye is positioned relatively far posterior to it). In *Scaphirhynchus*, the descending process is broad (as opposed to being a sharp point as in other genera) and in contact with the posterior border rostral bones (this was seen outside of *Scaphirhynchus* only on one side of one specimen of *A. brevirostrum*); this condition can be considered a synapomorphy of *Scaphirhynchus*, as suggested by Findeis (1997, character 61). Findeis (1997, character 46, in part) considered an elongate descending process to be a synapomorphy of *Scaphirhynchus* + *Pseudoscaphirhynchus*. However, because of the variation in the size of the descending process in *Acipenser* (short to relatively elongate) noted by Findeis and through our own observations and the fact that in *Pseudoscaphirhynchus* we never observed the process to contact the posterior border rostral bones, we reject it as a synapomorphy of Scaphirhynchini.

The way this character optimizes on the resulting phylogenies in our analysis differs between the two recovered topologies. In tree 1 (Fig. 128A), the absence of a supraorbital supports Acipenseriformes as a whole, and the presence of a supraorbital with a descending process is a character of Acipenseridae. Within acipenserids, then, the group †*Priscosturion* + *Scaphirhynchus* is supported by a supraorbital without a descending process (effectively the loss of the descending process), and *Scaphirhynchus* is defined by the

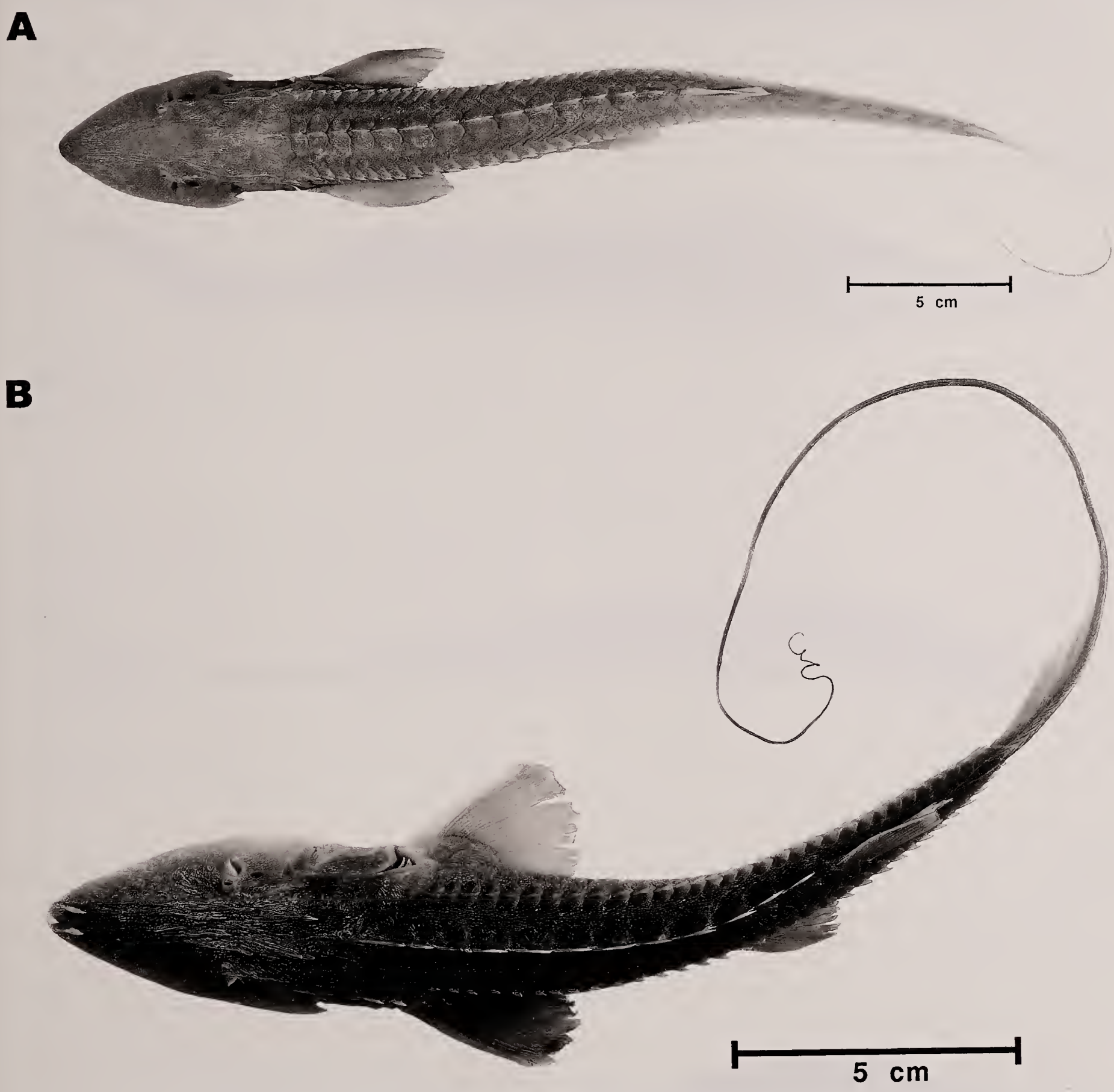


FIG. 113. Whole specimens of (**A**) *Scaphirhynchus platorynchus* (FMNH 45024; 290 mm SL) and (**B**) *Pseudoscaphirhynchus kaufmanni* (UAIC 13265.01, 188 mm SL) in dorsal view. Anterior to left.

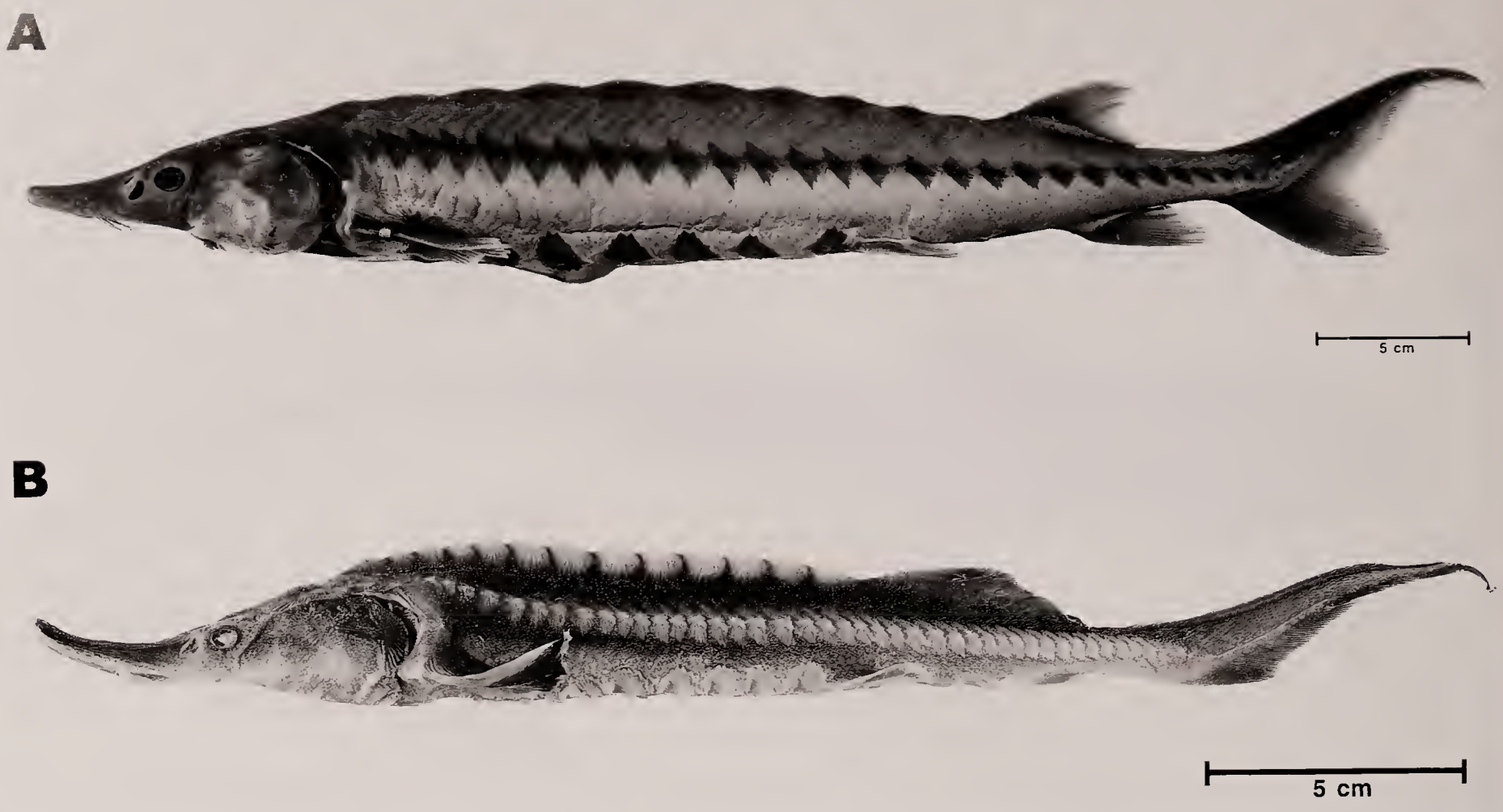


FIG. 114. Whole specimens of (**A**) *Acipenser brevirostrum* (MCZ 54265; 405 mm SL) and (**B**) *Huso huso* (MCZ 54269, 228 mm SL) in lateral view. Anterior to left.

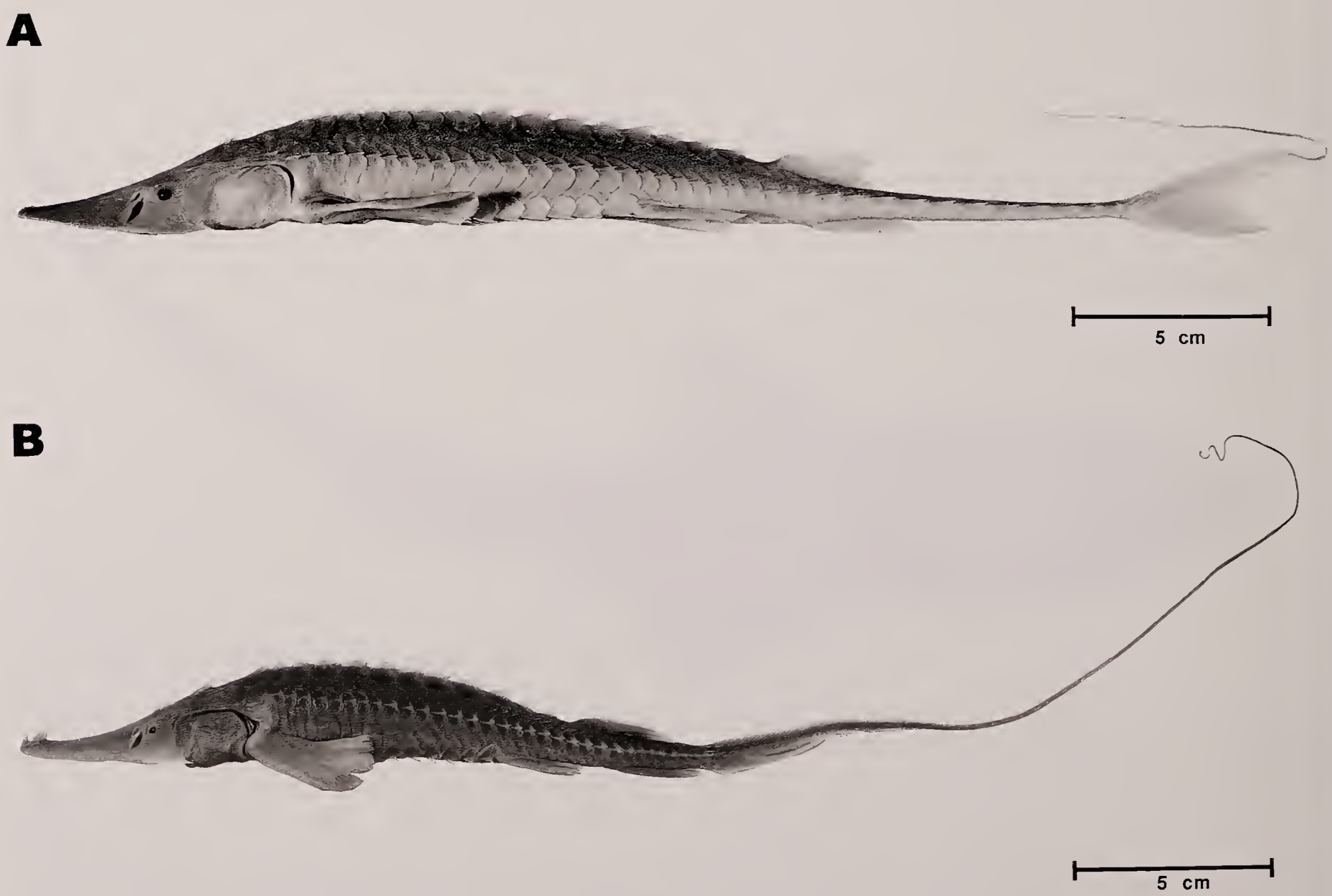


FIG. 115. Whole specimens of (**A**) *Scaphirhynchus platorynchus* (FMNH 45024; 290 mm SL) and (**B**) *Pseudoscaphirhynchus kaufmanni* (UAIC 13265.01, 188 mm SL) in lateral view. Anterior to left.

presence of a greatly expanded descending process. We regard the transformation of this character on the other topology (Fig. 128B) as much simpler and therefore more likely: the presence of a supraorbital without a descending process defines Acipenseridae, the presence of a supraorbital with a descending process supports all acipenserids except for †*Priscosturion*, and the expansion of the descending process is a character of *Scaphirhynchus*.

Character 10. Median extrascapular (0 = absent; 1 = present).

The presence of a median extrascapular was regarded as a synapomorphy of Acipenseridae by Findeis (1997, character 5). In all extant acipenserids, the median extrascapular is a large, triangular median bone of the extrascapular series; in the one known specimen of †*Priscosturion*, there is no median extrascapular (Grande & Hilton, 2006). A small median extrascapular was found to be present in all specimens of †*Chondrosteus* examined by Hilton and Forey (2009) that have this region clearly preserved. Grande et al. (2002) described a median extrascapular in the basal polyodontid †*Protopsephurus*. In our analysis, a median extrascapular was recovered either as a synapomorphy of Acipenseriformes, with reversals in †*Peipiaosteus*, *Polyodon*, and †*Priscosturion* (Fig. 128A), or as independently occurring in †*Chondrosteus*, †*Protopsephurus*, and Acipenseridae to the exclusion of †*Priscosturion* (Fig. 128B).

Character 11. Rostral canal (0 = straight; 1 = curves).

Findeis (1997, character 6) defined this character as a synapomorphy of the family Acipenseridae. In sturgeons, the infraorbital sensory canal continues anteriorly after exiting the jugal as the rostral sensory canal. The rostral canal courses anteriorly and arches laterally around the lateralmost set of barbels before continuing anteriorly toward the tip of the snout. In all out-groups studied here (condition unknown in †*Chondrosteus*; Hilton & Forey, 2009), the rostral sensory canal is straight along the ventral surface of the snout. †*Priscosturion* is coded as unknown because of a lack of preservation. As in Findeis's (1997) study, we found this character to be a synapomorphy of the family Acipenseridae.

Character 12. Dorsal rostral bone shape (0 = elongate and narrow; 1 = short and broad).

The individual bones of the dorsal rostral series of sturgeons are variable in their number, arrangement, and shape. However, even though the shape of individual elements is irregular, two overall forms can be distinguished: taxa with relatively elongate and narrow dorsal rostral bones and taxa with short and broad dorsal rostral bones. Although the distinction between the states of this character is admittedly subjective, we feel that two conditions are readily recognizable. Most species of *Acipenser* that we have examined have short, block-shaped dorsal rostral bones (e.g., *A. brevirostrum*, †*Priscosturion*; Fig. 130) that may be similar in general shape to that of the border rostral bones. In contrast, the dorsal rostral bones of other taxa (e.g., *H. huso*, *A. ruthenus*, *A. stellatus*, and *Pseudoscaphirhynchus*; Fig. 131) are relatively longer bones that are quite distinct from the border rostral bones (not present in *H. huso*), which may be more "stellate" in shape (e.g., *A. baerii*, not to be confused with the stellate bones of paddlefishes, although they may share some topographic correspondence; see the section Anamestic Bones of the Dorsal Rostrum) or broader elements, such as in *A. stellatus*, *Pseudoscaphirhynchus*, and *Scaphirhynchus*. Polyodontids are coded as having elongate dorsal rostral bones because of the possible correspondence between the elongate a, b, and c bones (Grande & Bemis, 1991) and the dorsal rostral bones of acipenserids. The presence of elongate dorsal rostral bones is considered plesiomorphic for Acipenseridae.

In our analysis, the presence of short, broad dorsal rostral bones is interpreted as a synapomorphy of the group (*A. oxyrinchus*, *A. transmontanus* [{†*Priscosturion* + *Scaphirhynchus*} + {*A. brevirostrum* + *A. fulvescens*}]) (Fig. 128A), or the presence of short dorsal rostral bones supports Acipenseridae with a change to elongate dorsal rostral bones in the group ([*A. baerii* + {*H. huso* + *A. ruthenus*}] + [*A. stellatus* + *Pseudoscaphirhynchus*]) (Fig. 128B).

Character 13. Spines on dermal skull bones (0 = absent; 1 = present)

In his analysis, Findeis (1997, character 41) found the condition of having spines in the center of the parietal, posttemporal, supracleithrum, and anterior dorsal rostral bones to be a synapomorphy of *Scaphirhynchus* + *Psendoscaphirhynchus*. Contrary to Findeis (1997, p. 107), who wrote that "some skull bones of *Acipenser* possess central ridges, but never manifest spines and anterior dorsal rostral bones are plates without raised ridges or spines. *Huso* never possesses spines or strong ridges in any skull bones," we discovered similar spine patterns to those in *Scaphirhynchus* and *Pseudoscaphirhynchus* in all our specimens of *A. stellatus* that we examined as well as in juvenile specimens of *Huso* (although we coded this taxon as 0 because in specimens approximately 1 m SL lack spines on the skull bones, so it is regarded as an ontogenetically variable character). In both fundamental cladograms resulting from our analysis, the presence of spines on the dermal bones of the skull is found independently in *Scaphirhynchus* and in the clade *A. stellatus* + *Pseudoscaphirhynchus*. Interestingly, the shape of these spines in the two groups differs slightly, with those of *Scaphirhynchus* being slightly conical and the spines of the other taxa being narrow, thorn-shaped processes.

Findeis (1997, character 55) defined a related character, the presence of "spikes" on the frontals, which he found to be a synapomorphy of *Pseudoscaphirhynchus* (although by his own admission the derived condition was found only in *P. kaufmanni*). Because of the variation within *Pseudoscaphirhynchus* and the subjective nature of the distinction between "spines" and "spikes," we did not include this second character in our analysis.

Character 14. Trunk, occipital, supraorbital lateral lines (0 = meet in posttemporal; 1 = meet in lateral extrascapular).

Findeis (1997, character 56) considered the joining of these three sensory canals in the lateralmost bone of the extrascapular series to be a synapomorphy of *Pseudoscaphirhynchus*. However, among acipenserids, we also found this condition in *A. stellatus* and †*Priscosturion*. Additionally, having these canals join in the lateral extrascapular is widespread in nonacipenserid Acipenseriformes as well as other basal actinopterygians. In our analysis, the confluence of the trunk, occipital, and supraorbital canals in the posttem-

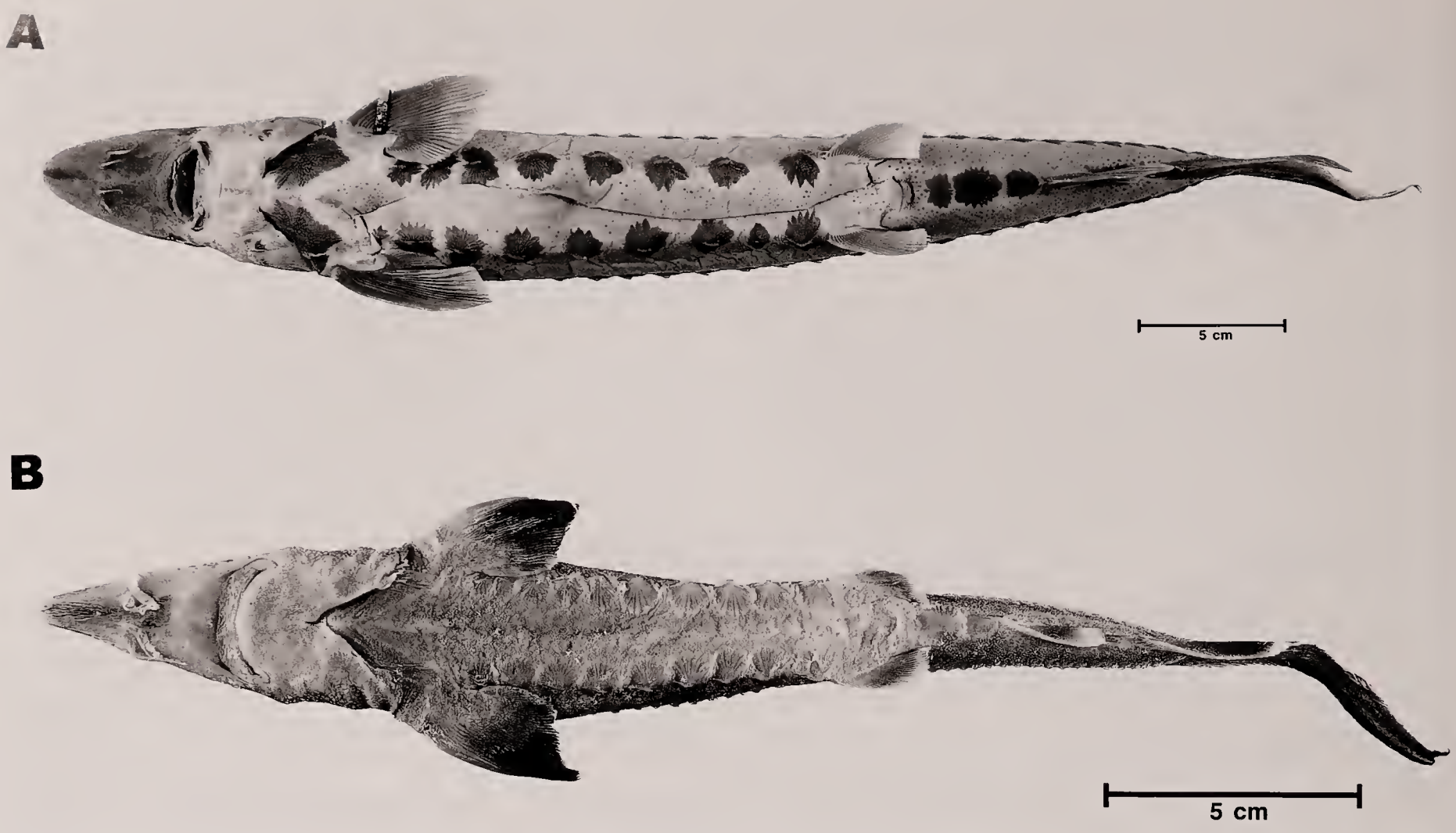


FIG. 116. Whole specimens of (**A**) *Acipenser brevirostrum* (MCZ 54265; 405 mm SL) and (**B**) *Huso huso* (MCZ 54269, 228 mm SL) in ventral view. Anterior to left.

poral is considered to be a synapomorphy of either all sturgeons above the clade *A. stellatus* + *Pseudoscaphirhynchus*, with a reversal in †*Priscosturion* (Fig. 128A), or all sturgeons above †*Priscosturion* and a reversal in the clade *A. stellatus* + *Pseudoscaphirhynchus* (Fig. 128B).

Character 15. Posterior elongation of parasphenoid (0 = absent; 1 = present).

In all Acipenseriformes, the posterior rami of the parasphenoid extend to (*Polyodon*) or posterior to (all other taxa) the parietal bones (here considered state 1; from Grande et al., 2002, character 2). In †*Birgeria* the parasphenoid extends posteriorly to reach the occipital region (Neilson, 1949) and is coded as 1. On both most-parsimonious cladograms, the posterior elongation of the parasphenoid is found to be a synapomorphy of †*Birgeria* + Acipenseriformes.

Character 16. Ascending process of parasphenoid (0 = extends perpendicularly; 1 = extends anteriorly; 2 = extends posteriorly).

In ventral view, the angle formed by the main axis of the ascending processes of the parasphenoid (relative to the main body of the parasphenoid) is variable within Acipenseriformes. In out-groups (Neilson, 1949), †*Chondrosteus* (Hilton & Forey, 2009), †*Peipiaosteus* (Grande & Bemis, 1996; Fig. 132A) and †*Priscosturion* (Grande & Hilton, 2006; Fig. 132C), the ascending processes extend posteriorly to a varying degree (cf. Figs. 132A and 132C). In polyodontids, the ascending processes extend from the body of the parasphenoid more or less perpendicularly (e.g., *Polyodon*; Fig. 132B). In all extant acipenserids (e.g., Fig. 132D, E), the ascending processes are directed anteriorly. This character (state 1) supports either all Acipenseridae with a reversal (to state 2) in †*Priscosturion* (Fig. 128A) or as a synapomorphy of all Acipenseridae except †*Priscosturion* (Fig. 128B).

Character 17. Median anterior process of the parasphenoid (0 = absent; 1 = present).

The median anterior process of the parasphenoid is a distinct extension of this bone along the anterior midline of the snout. This process is not present in †*Peipiaosteus* (Fig. 132A), *Polyodon* (because of the ventral rostral bones, this absence is not apparent in Fig. 132B), or the nonacipenseriform taxa in our matrix, but it is well developed in †*Chondrosteus* (Hilton & Forey, 2009, fig. 8), †*Protopsephurus* (Grande et al., 2002, fig. 7), and all Acipenseridae examined (e.g., Fig. 132C–E). In both topologies recovered in our analysis, the presence of the median anterior process of the parasphenoid supports Acipenseriformes, with independent losses in †*Peipiaosteus* and *Polyodon*. However, the precise distribution of this character needs further study, as there is variation within polyodontids (e.g., present in †*Protopsephurus* and †*Crossopholis* but absent in *Polyodon* and probably absent in *Psephurus* and †*Palaeopsephurus*; see figures in Grande & Bemis, 1991). Note also that the condition in †*Crossopholis* is different than that found in acipenserids in that the anterior process is only slightly differentiated from the anterior portion of the parasphenoid and is much broader than in other taxa, including †*Protopsephurus*; therefore, further determination of the morphological correspondence is warranted.

FIG. 117. Whole specimens of (**A**) *Scaphirhynchus platorynchus* (FMNH 45024; 290 mm SL) and (**B**) *Pseudoscaphirhynchus kaufmanni* (UAIC 13265.01, 188 mm SL) in ventral view. Anterior to left.

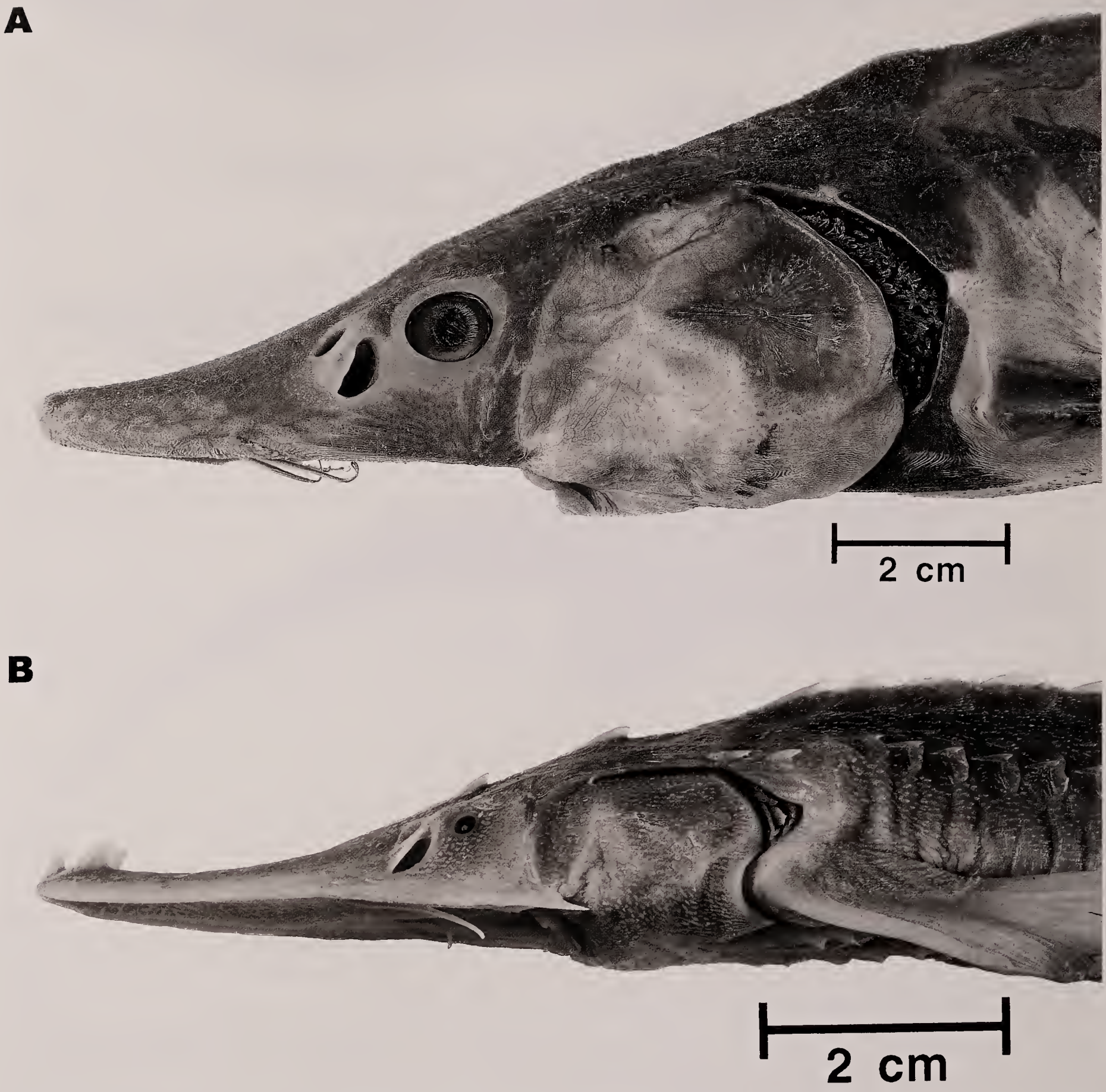


FIG. 118. Heads of (**A**) *Acipenser brevirostrum* (MCZ 54265; 405 mm SL) and (**B**) *Pseudoscaphirhynchus kaufmanni* (UAIC 13265.01, 188 mm SL) in lateral view. Note the presence of the spiracle in *Acipenser*. The absence of the spiracle in *Pseudoscaphirhynchus* is ontogenetically variable (i.e., present in larvae and small individuals, closed in adults); the spiracle is always closed in *Scaphirhynchus* (Findeis, 1993). Anterior to left.

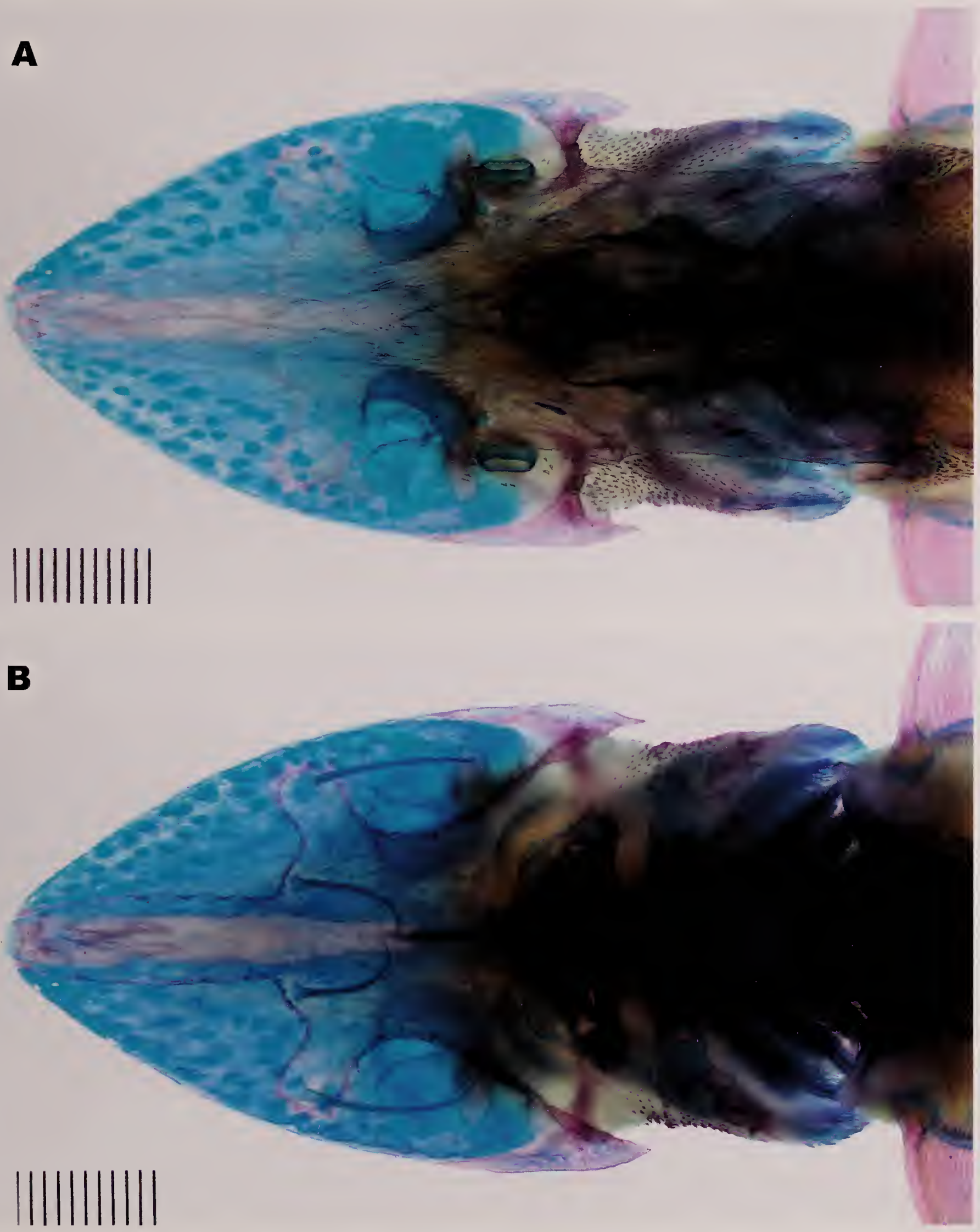


FIG. 119. *Scaphirhynchus platorynchus* (VIMS 12098, 250 mm SL), cleared and stained skull and pectoral girdle in (**A**) dorsal and (**B**) ventral views. Scale in millimeters. Anterior to left.

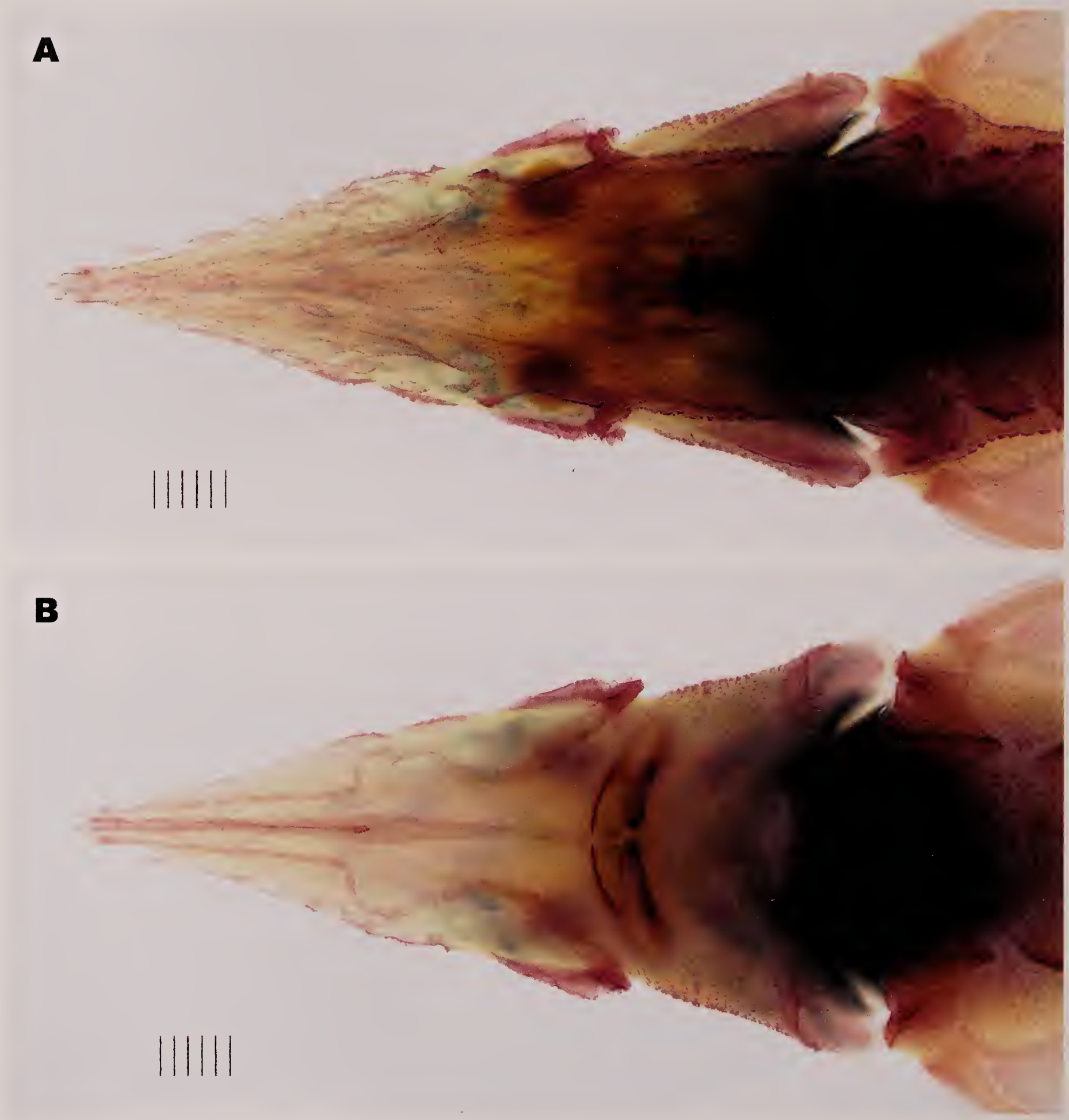


FIG. 120. *Acipenser fulvescens* (UMMZ 223764, 185 mm SL), cleared and stained skull and pectoral girdle in (**A**) dorsal and (**B**) ventral views. Scale in millimeters. Anterior to left.

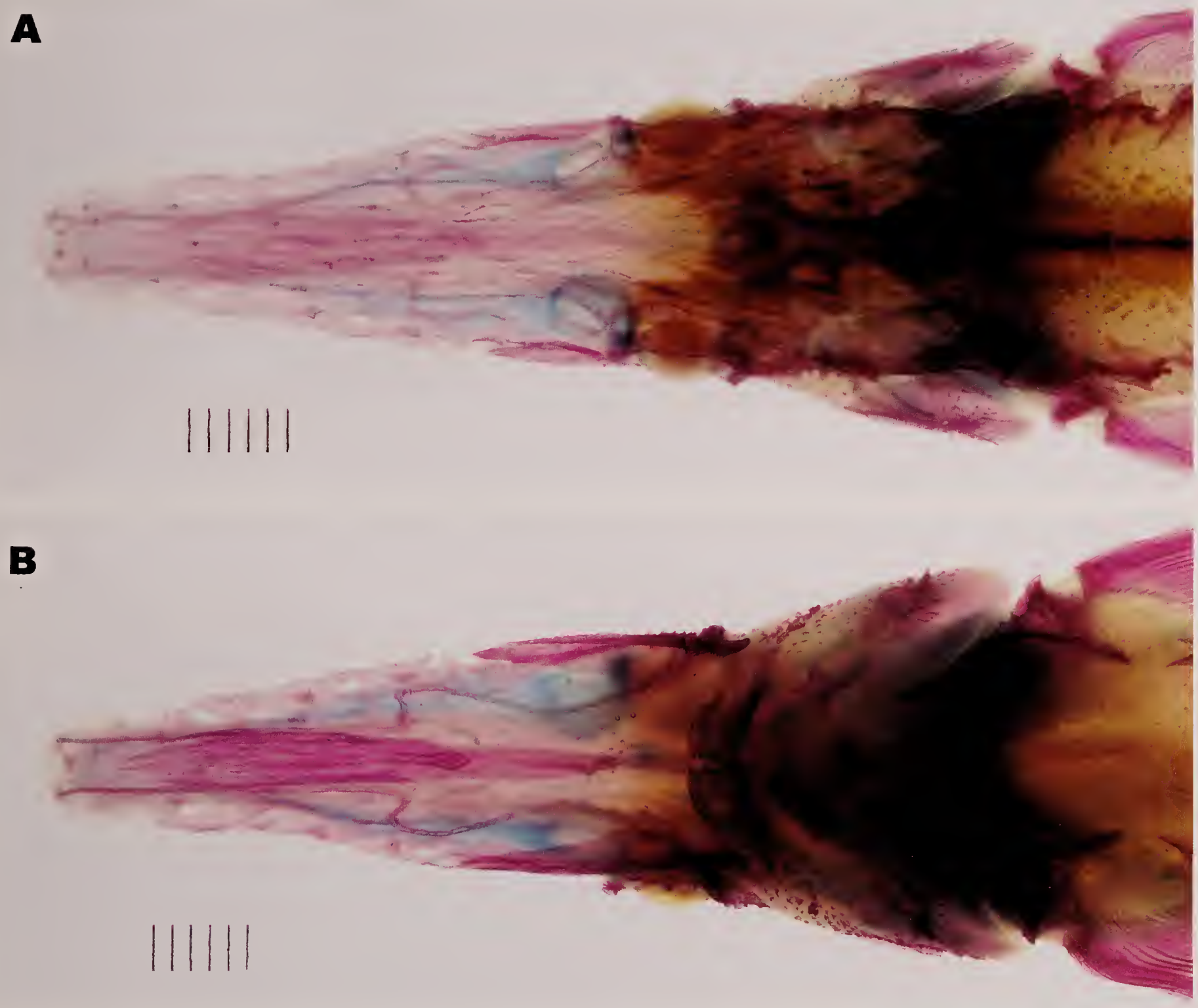


FIG. 121. *Acipenser stellatus* (UMMZ 184980, 160 mm SL), cleared and stained skull and pectoral girdle in (**A**) dorsal and (**B**) ventral views. Scale in millimeters. Anterior to left.

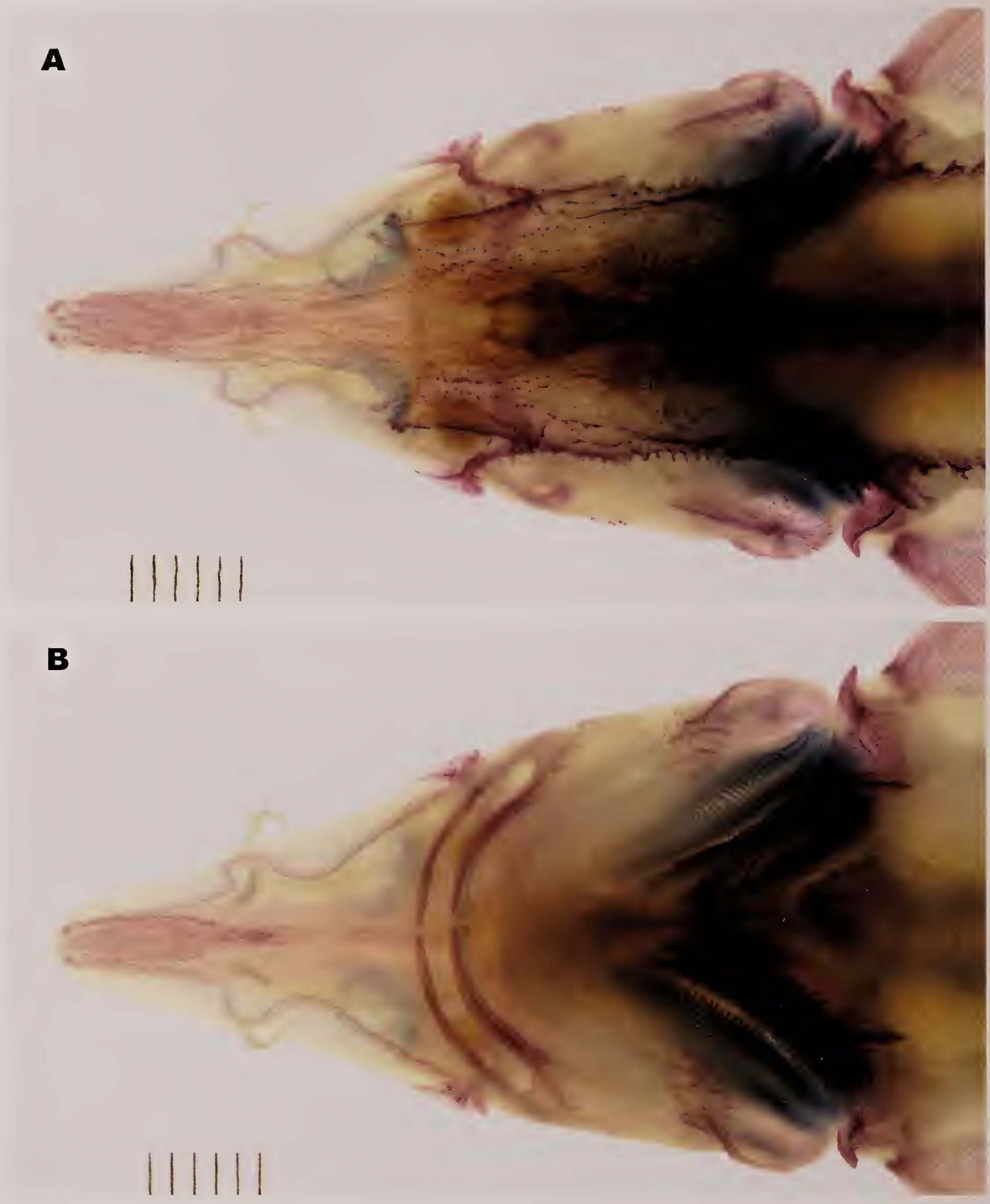


FIG. 122. *Huso huso* (CAS 211810, 130 mm SL), cleared and stained skull and pectoral girdle in (**A**) dorsal and (**B**) ventral views. Scale in millimeters. Anterior to left.

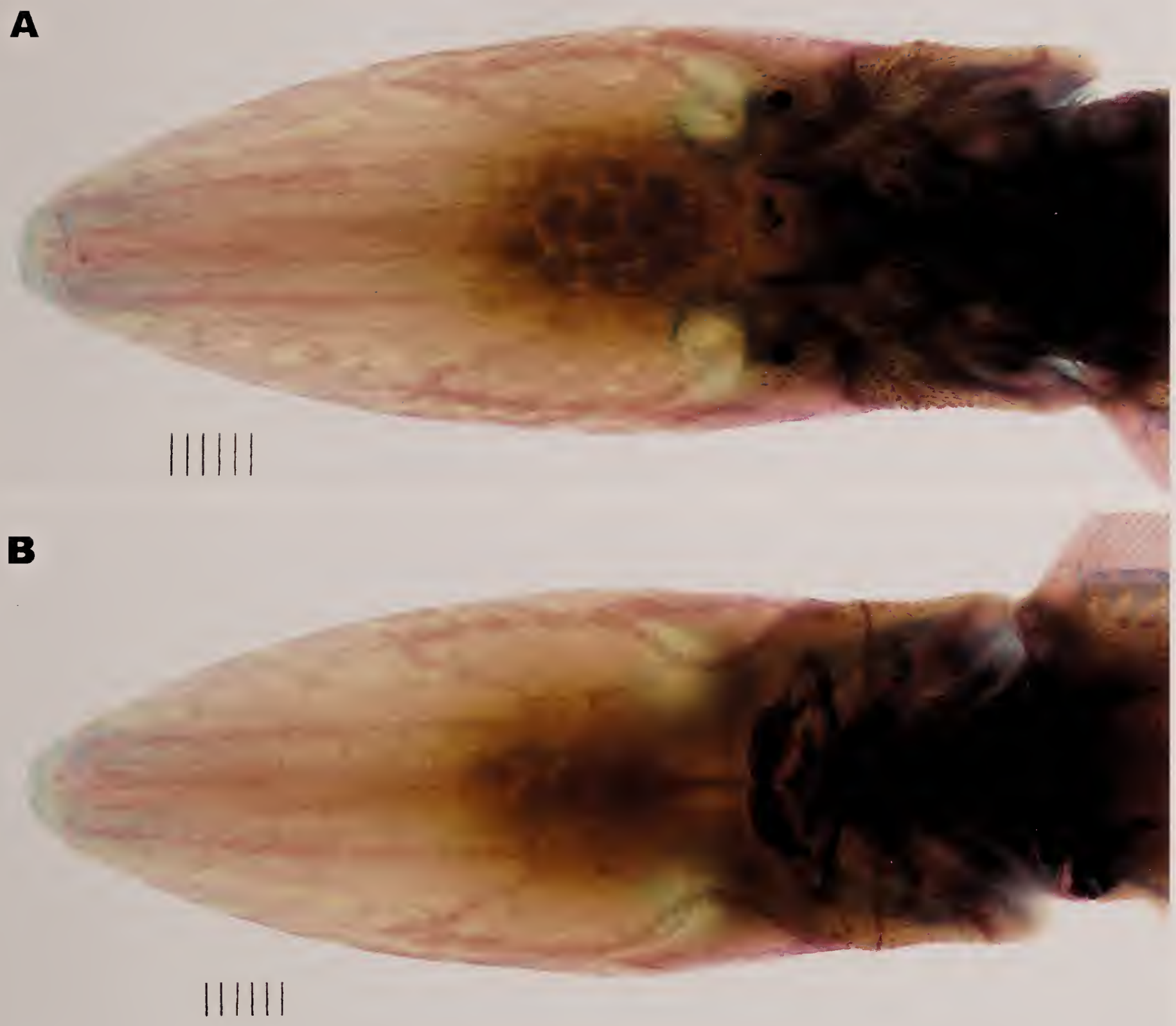


FIG. 123. *Pseudoscaphirhynchus hermanni* (uncataloged, 182 mm SL), cleared and stained skull and pectoral girdle in (**A**) dorsal and (**B**) ventral views. Scale in millimeters. Anterior to left.

TABLE 9. Species of sturgeons (Acipenseridae) considered valid, following Birstein and Bemis (1997) and Hilton and Grande (2006).

Taxon	Distribution
†*Priscosturion longipinnis* (Grande & Hilton, 2006)	Late Cretaceous, Montana
†*Protoscaphirhynchus squamosus* Wilimovsky, 1956	Late Cretaceous, Montana
Acipenser sturio Linnaeus, 1758	Ponto-Caspian region; northeastern Atlantic
Acipenser ruthenus Linnaeus, 1758	Ponto-Caspian region; northeastern Atlantic; Arctic Ocean
Acipenser stellatus Pallas, 1771	Ponto-Caspian region
Acipenser oxyrinchus Mitchill, 1815	St. Lawrence River; northwestern Atlantic; Gulf of Mexico
Acipenser fulvescens Rafinesque, 1817	Great Lakes, Hudson Bay, and St. Lawrence River regions
Acipenser brevirostrum Lesueur, 1818	northwestern Atlantic
Acipenser nudiventris Lovetzky, 1828	Ponto-Caspian region
Acipenser gueldenstaedtii Brant & Ratzeberg, 1833	Ponto-Caspian region
Acipenser sinensis Gray, 1834	China
Acipenser naccarii Bonaparte, 1836	Ponto-Caspian region
Acipenser dabryanus Duméril, 1869	China
Acipenser transmontanus Richardson, 1836	northeastern Pacific
Acipenser medirostris Ayres, 1854	northeastern Pacific
Acipenser schrenkii Brandt, 1869	Amur River
Acipenser baerii Brandt, 1869	Siberia; Arctic Ocean
Acipenser mikadoi Hilgendorf, 1892	northwestern Pacific
Acipenser persicus Borodin, 1897	Ponto-Caspian region
Huso huso (Linnaeus, 1758)	Ponto-Caspian region
Huso dauricus (Georgi, 1775)	Amur River; northwestern Pacific
Scaphirhynchus platorhynchus (Rafinesque, 1820)	Mississippi River region
Scaphirhynchus albus (Forbes & Richardson, 1905)	Mississippi River region
Scaphirhynchus suttkusi Williams & Clemmer, 1991	Alabama
Pseudoscaphirhynchus fedtshenkoi (Kessler, 1872)	Ponto-Caspian region
Pseudoscaphirhynchus kaufmanni (Bogdanov, 1874)	Ponto-Caspian region
Pseudoscaphirhynchus hermanni (Sewertzoff in Kessler, 1877)	Ponto-Caspian region

Character 18. Ventral rostral bones (0 = absent; 1 = present).

The ventral rostral bones of Acipenseriformes form the series of elements that contact the anterior point of the median anterior process of the parasphenoid posteriorly and extend anteriorly to terminate at the tip of the snout. These are intraspecifically variable in number, shape, and position. The bones found in acipenserids and †*Protopsephurus* are considered homologous to the p, v, and cv bones labeled by Grande and Bemis (1991) in polyodontids. The relationship of these bones to the vomers described in polyodontids by Grande and Bemis (1991) is unclear, although in this analysis we considered the "vomers" in polyodontids to be part of this series, following Findeis (1997, p. 101). The presence of these bones was found to be a synapomorphy of Acipenseridae + Polyodontidae by Grande et al. (2002, character 20), as it was in our analysis.

Character 19. Posteriormost ventral rostral bone (0 = paired; 1 = single).

Findeis (1997, character 30) considered that a paired condition of the posteriormost ventral rostral bone was plesiomorphic and that the presence of a single bone in this position was a synapomorphy of the clade of all acipenserids to the exclusion of *Huso*, which he found to have the paired condition (also found in polyodontids). In specimens of *H. huso* studied here (e.g., CAS 211810, 130 mm SL), there is a single ventral rostral bone in this position, suggesting that this character is polymorphic in this species. Therefore, the presence of a single posteriormost ventral rostral bone is interpreted in our analysis to be a synapomorphy of the family Acipenseridae. For those taxa in which ventral rostral bones are absent, this character was coded as not applicable.

Character 20. Ventral surface of posteriormost ventral rostral bone (0 = keeled; 1 = flat).

Findeis (1997, character 42) defined a binary character describing the length of the posteriormost ventral rostral bone (with the cutoff between the states two-thirds the length of the ventral rostral series) as a synapomorphy of *Scaphirhynchus* + *Pseudoscaphirhynchus* (i.e., the presence of a posteriormost ventral rostral bone more than two-thirds the length of the entire series was a synapomorphy of Scaphirhynchini). The qualitative aspect of this character, which was noted by Findeis (1997, p. 107), makes it somewhat problematic, and there is more variation in the form of these bones than previously realized. We recognize the length difference that was described by Findeis (1997). The length of the ventral rostral bone in *Scaphirhynchus* (Fig. 132D) clearly is exaggerated and is unusual within extant acipenserids, with the exception of *P. kaufmanni*, which approaches the proportional length of *Scaphirhynchus*. We found the condition in the genus *Pseudoscaphirhynchus*, however, to be variable: the posteriormost element of the series in *P. hermanni* is only about half the length of the overall series, whereas that of *P. kaufmanni* is proportionately longer. In addition, the posteriormost element in *A. stellatus* is much longer than in most species of *Acipenser* and *Huso*. The posteriormost ventral rostral bone in †*Priscosturion* (Fig. 132C) appears to be even more elongated than *Scaphirhynchus*, although no bones anterior to this element are preserved (Grande & Hilton, 2006). In †*Priscosturion*, the anterior margin of this bone comes close to the tip of the snout, and if any more anterior ventral rostral bones were present, the posteriormost bone comprised well over half the length of the series.

In our analysis, we redefined the character to focus on the qualitative aspects of the posteriormost ventral rostral bone itself rather than emphasizing the difference in length (although

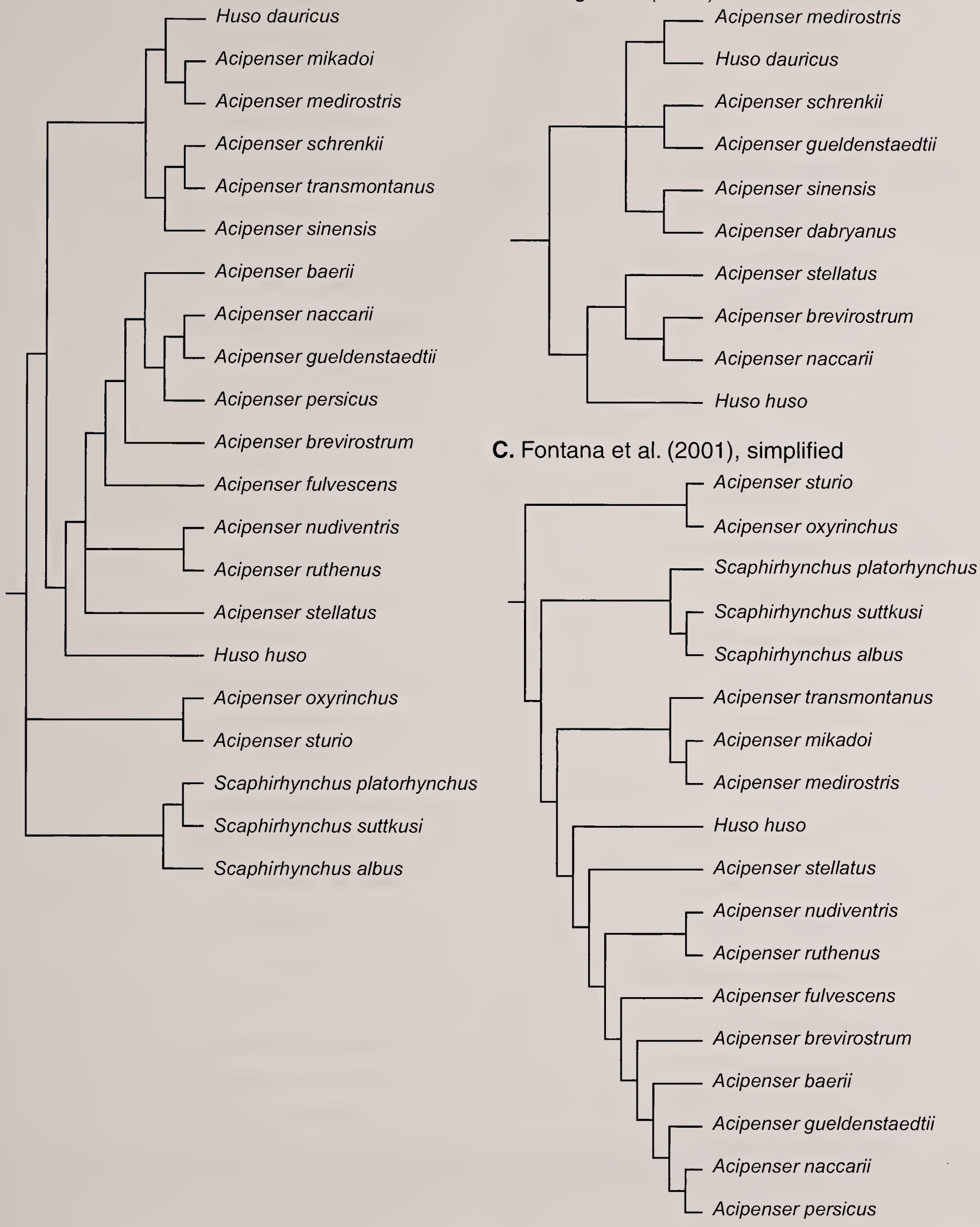


FIG. 124. Molecular phylogenetic hypotheses of relationships within Acipenseridae. (**A**) Ludwig et al. (2001, fig. 4) based on maximum parsimony analysis of the entire sequence of the cytochrome *b* gene. (**B**) Zhang et al. (2000, fig. 3) based on a maximum parsimony analysis of sequences of mtDNA ND4L-ND4 genes. (**C**) Simplified from Fontana et al. (2001, fig. 1) based on UPGMA analysis of cytochrome *b* sequences. Although removed from this figure for purposes of comparison, note that multiple individuals of several species were used in Fontana et al.'s analysis and the monophyly of *A. gueldenstaedtii* (relative to *A. naccarii* and *A. persicus*) was not supported.

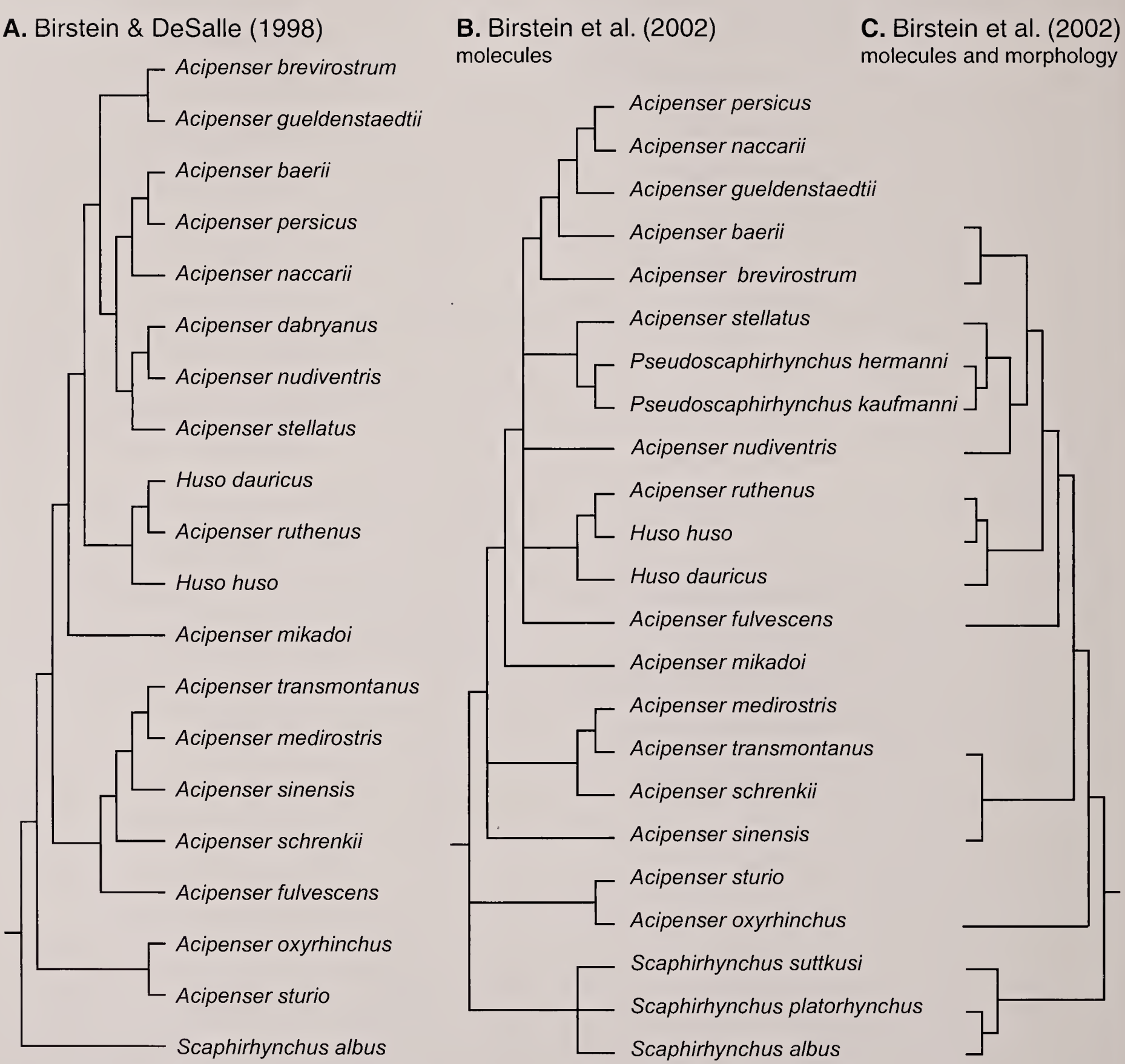


FIG. 125. Molecular phylogenetic hypotheses of relationships within Acipenseridae. (**A**) Birstein and DeSalle (1998, fig. 2) from analysis of cytochrome *b* and 12S and 16S mtrRNA genes. (**B**) Birstein et al. (2002, fig. 1A), maximum parsimony analysis of cytochrome *b*, NADH5, control region, and 12S and 16S mtrRNA genes. (**C**) Birstein et al. (2002, fig. 2A), maximum parsimony of combined genetic and morphological (from Mayden & Kuhajda, 1996) data.

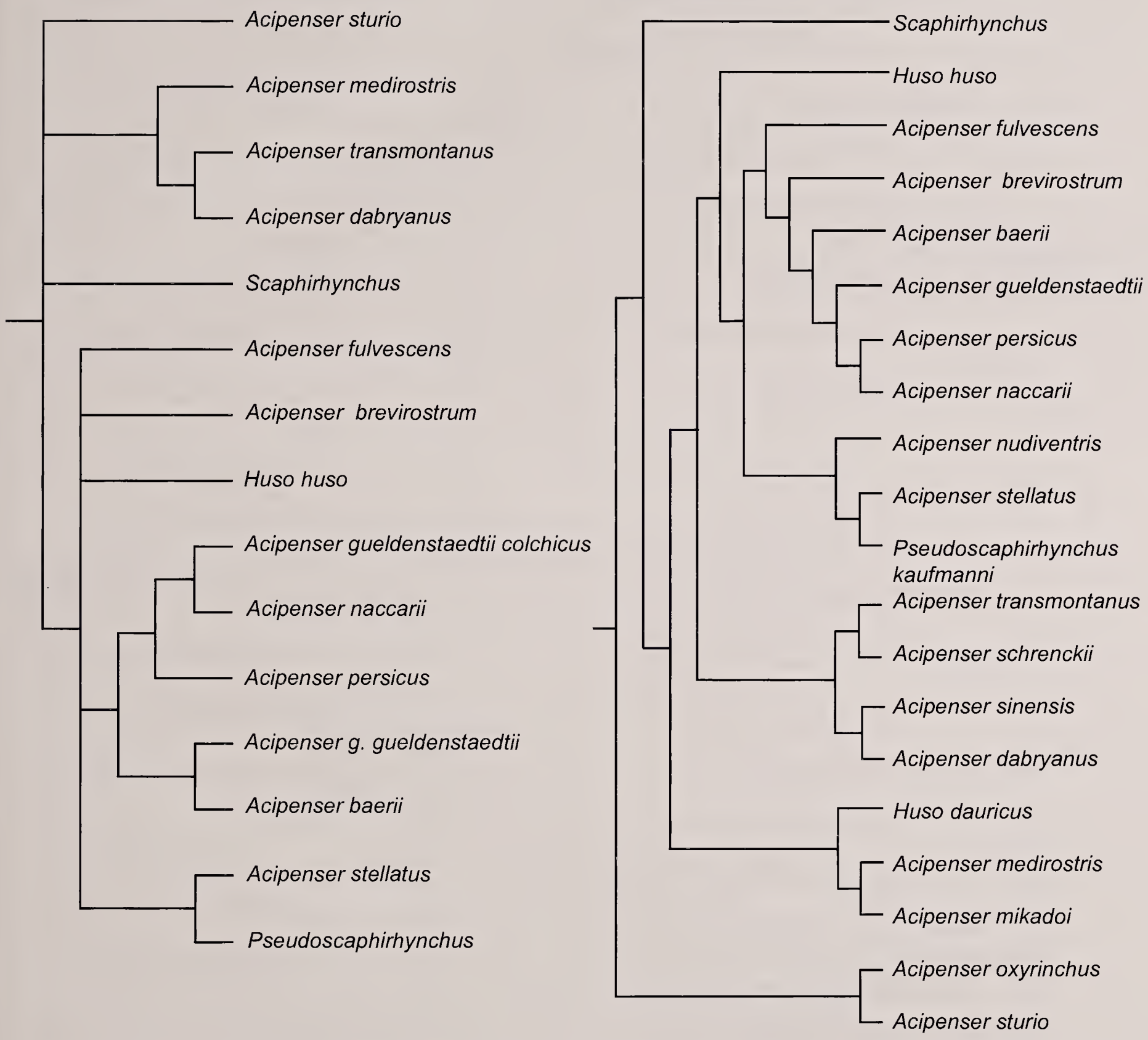
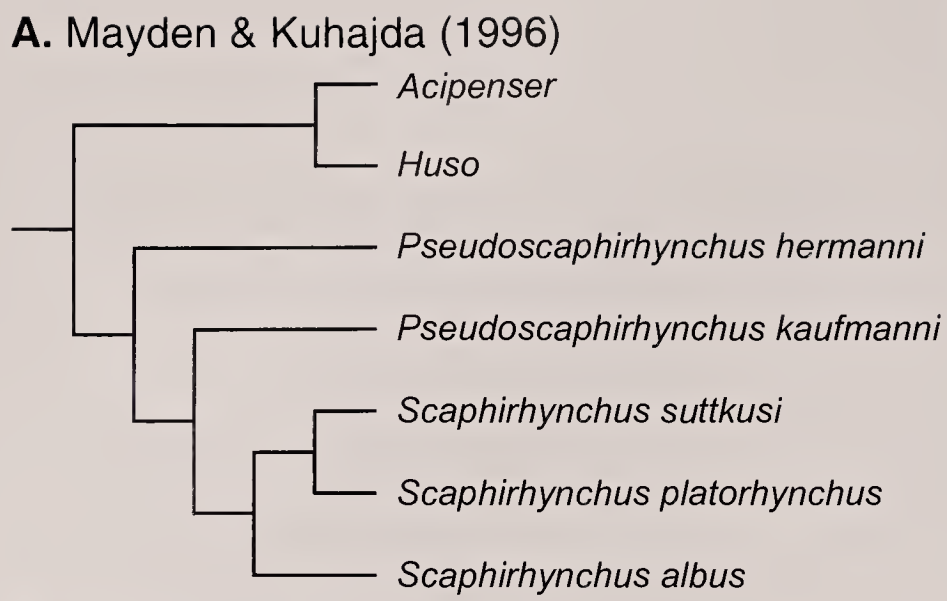
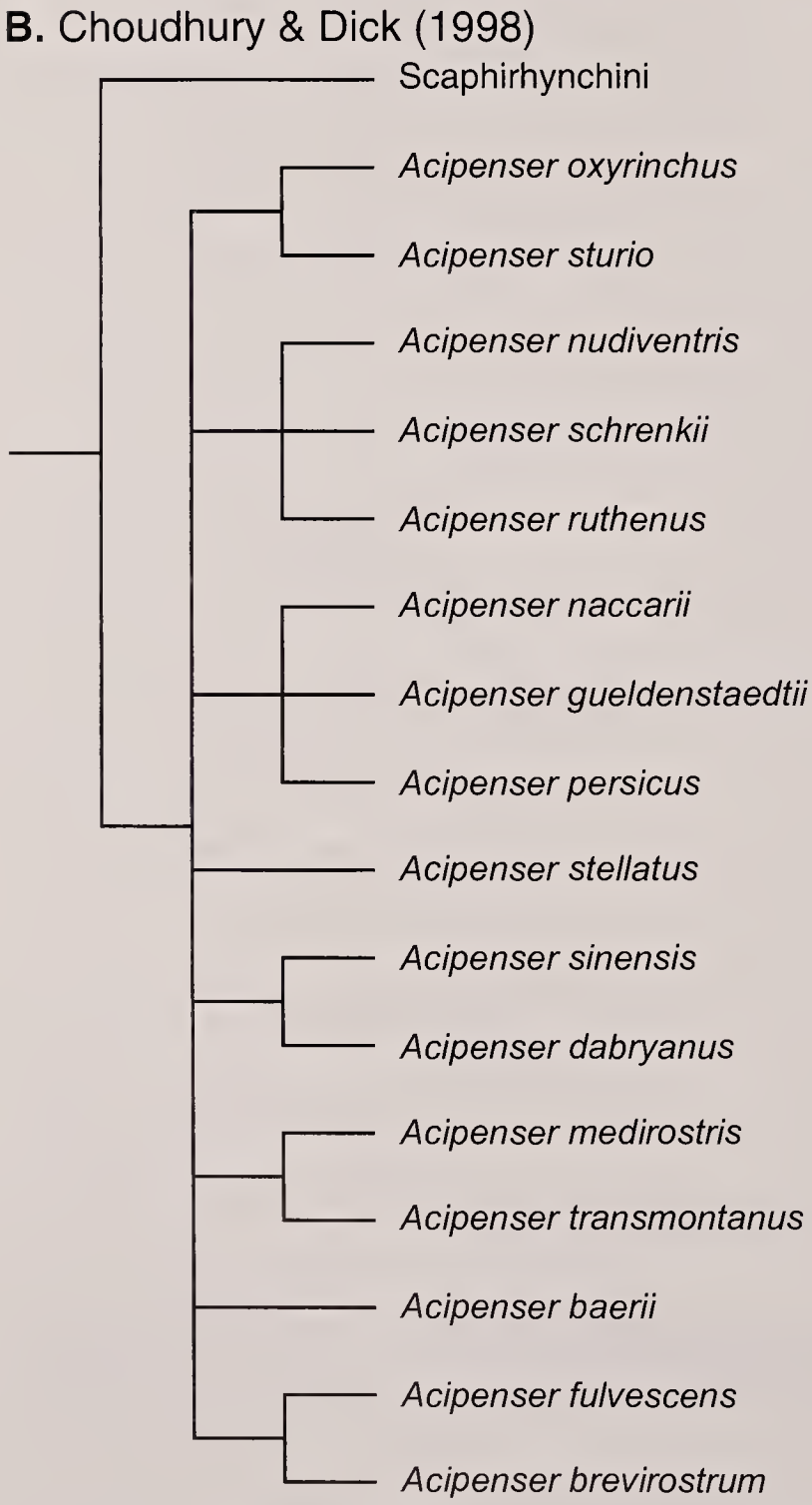


FIG. 126. Molecular phylogenetic hypotheses of relationships within Acipenseridae. (**A**) Dillman et al. (2007, fig. 1) from parsimony analysis of control region and cytochrome *b*. (**B**) Krieger et al. (2008, fig. 1) from maximum likelihood analysis of cytochrome *b*, 12S rRNA, cytochrome *c* oxidase subunit II, $tRNA_{Phs}$, $tRNA_{Asp}$, 16S rRNA, NADH5, and control region.





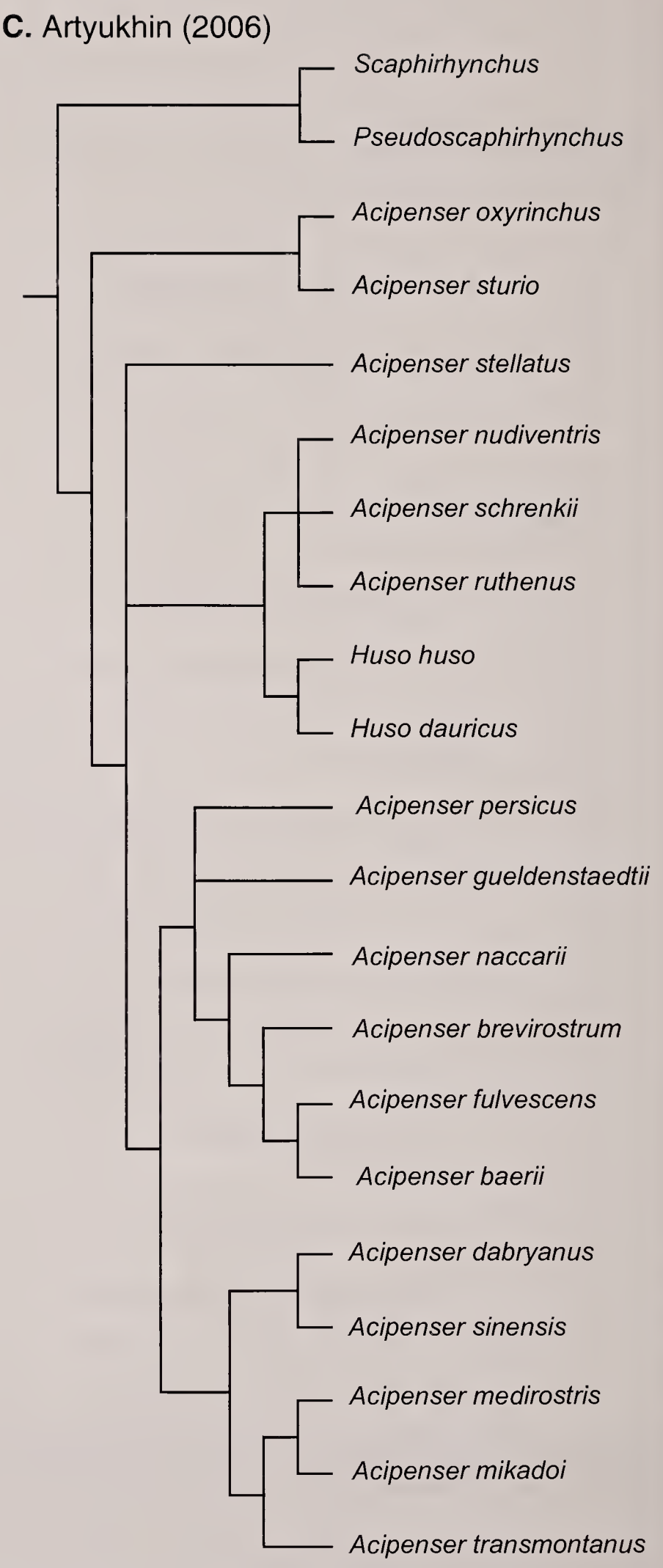


FIG. 127. Morphological phylogenetic hypotheses of relationships within Acipenseridae. (**A**) Mayden and Kuhajda (1996, fig. 9). (**B**) Choudhury and Dick (1998, fig. 4); based in part on Artyukhin (1995). (**C**) Artyukhin (2006, fig. 3).

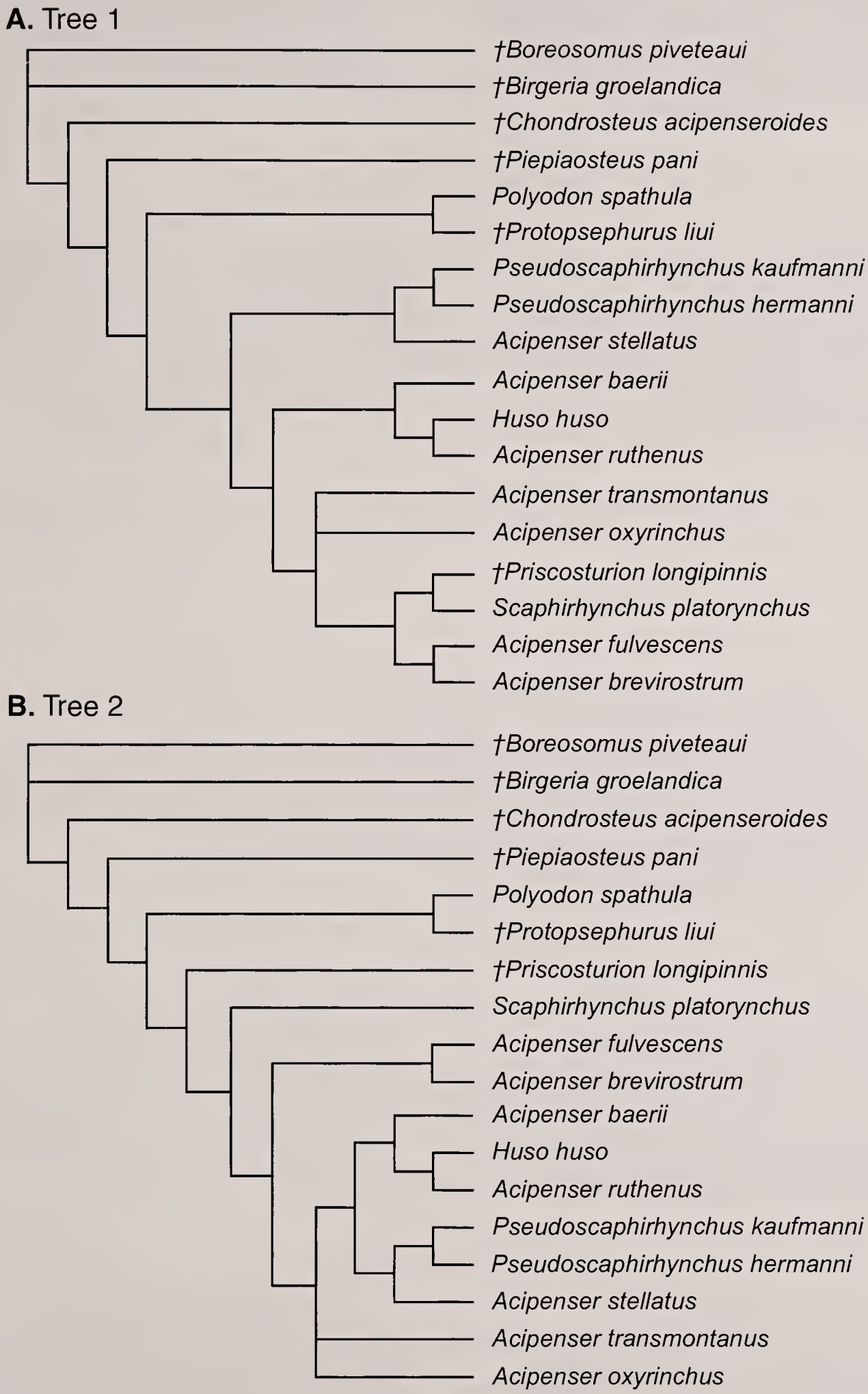


FIG. 128. The two most-parsimonious topologies based on analysis of the data matrix presented in Appendix II. These trees have a length of 106 steps, a consistency index (CI) of 0.6792 (0.6344 excluding uninformative characters), a homoplasy index (HI) of 0.3208 (0.3656 excluding uninformative characters), a retention index (RI) of 0.7901, and a rescaled consistency index (RC) of 0.5367. For strict consensus, see Figure 129.

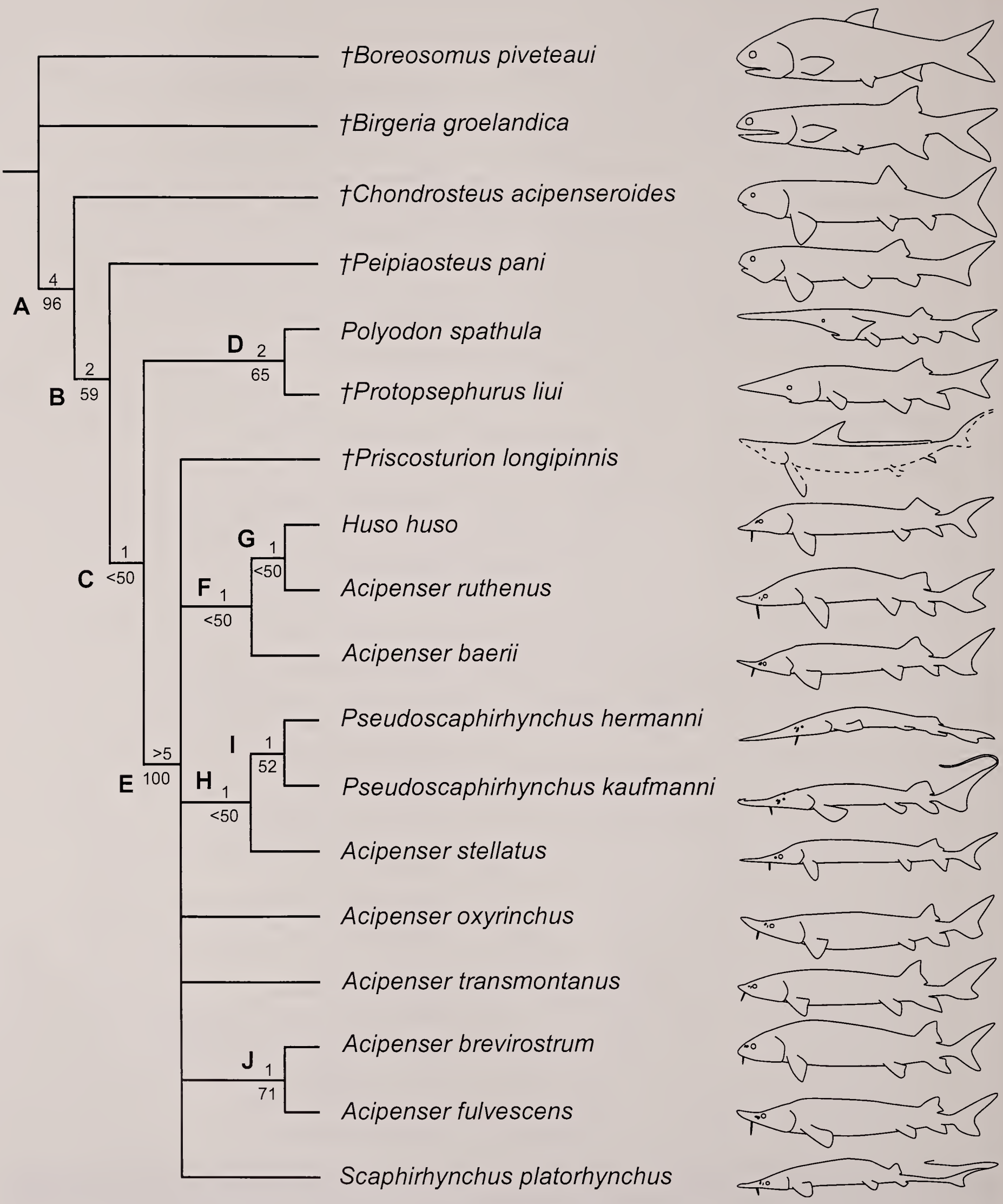


FIG. 129. Strict consensus phylogeny based on analysis of the data matrix presented in Appendix II. Numbers above the nodes are Bremer support values (calculated by searching for sub–most-parsimonious trees in PAUP*), and numbers below the nodes are bootstrap support values (1000 replicates, as calculated by PAUP*). See text for discussion of character support.

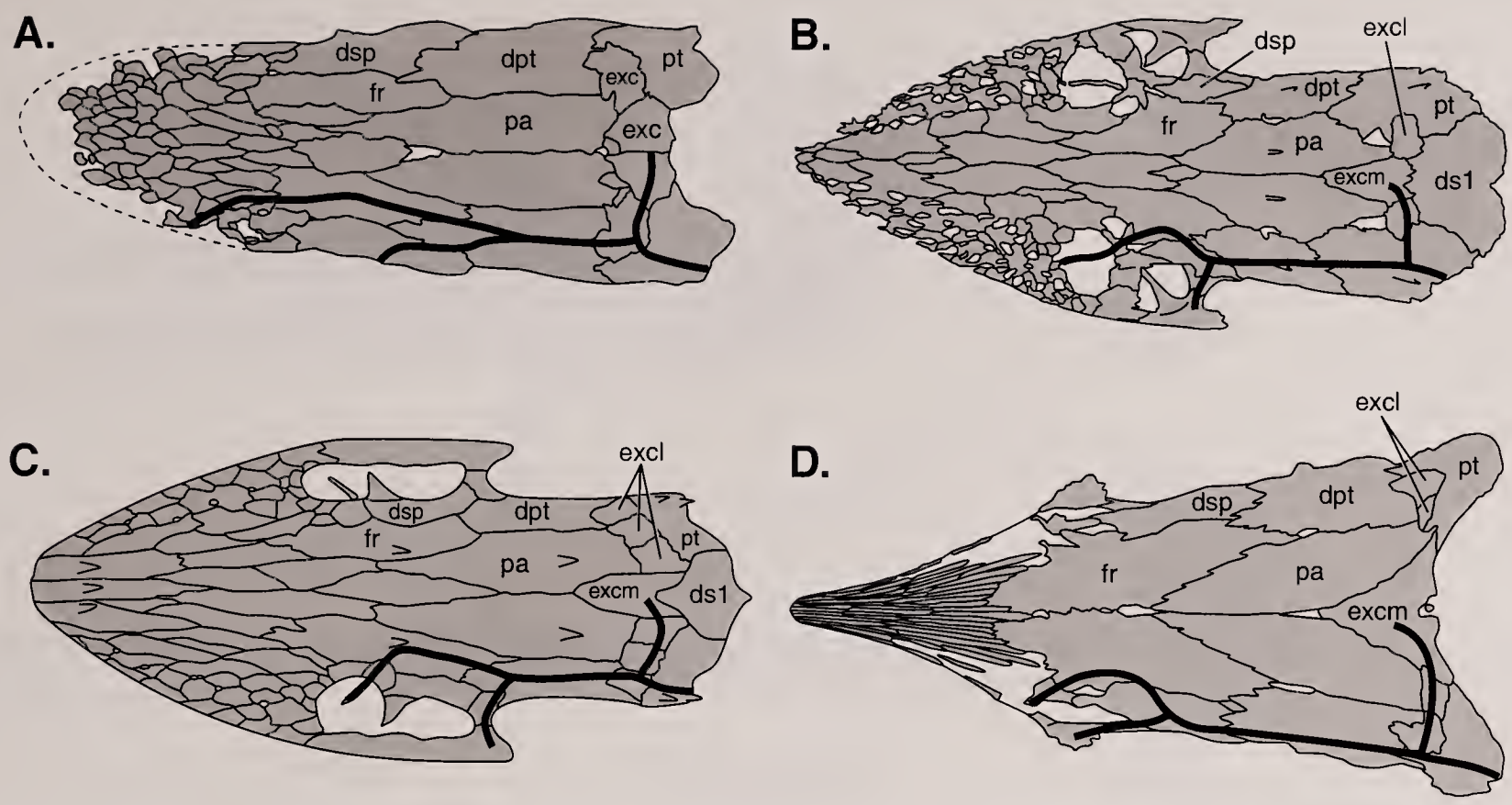


FIG. 130. Diagrammatic illustrations of the skull roof of sturgeons. (**A**) †*Priscosturion longipinnis* (after Grande & Hilton, 2006, fig. 6). (**B**) *Scaphirhynchus platorynchus* (after Findeis, 1993, fig. 15). (**C**) *Pseudoscaphirhynchus kaufmanni* (after Sewertzoff, 1926c, fig. 38). (**D**) *Huso huso* (after Kittary, 1850, pl. 7, fig. 7). Abbreviations found on pages 8–9.

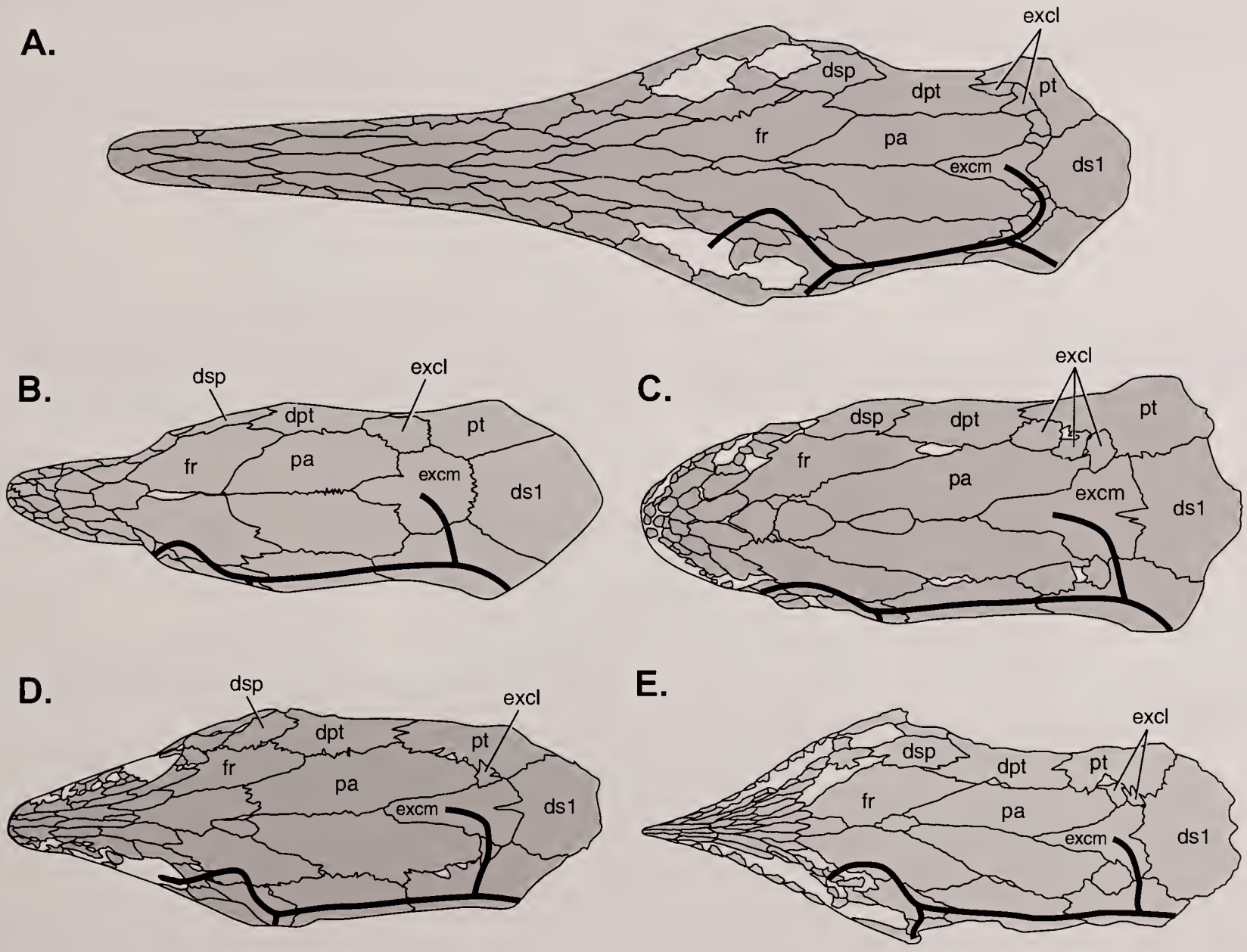


FIG. 131. Diagrammatic illustrations of the skull roof of sturgeons. (**A**) *Acipenser stellatus* (after Kittary, 1850, pl. 7, fig. 5). (**B**) *Acipenser oxyrinchus* (VIMS uncataloged). (**C**) *Acipenser transmontanus* (FMNH uncataloged). (**D**) *Acipenser baerii* (VIMS 12083). (**E**) *Acipenser ruthenus* (after Kittary, 1850, pl. 7, fig. 1). Abbreviations found on pages 8–9.

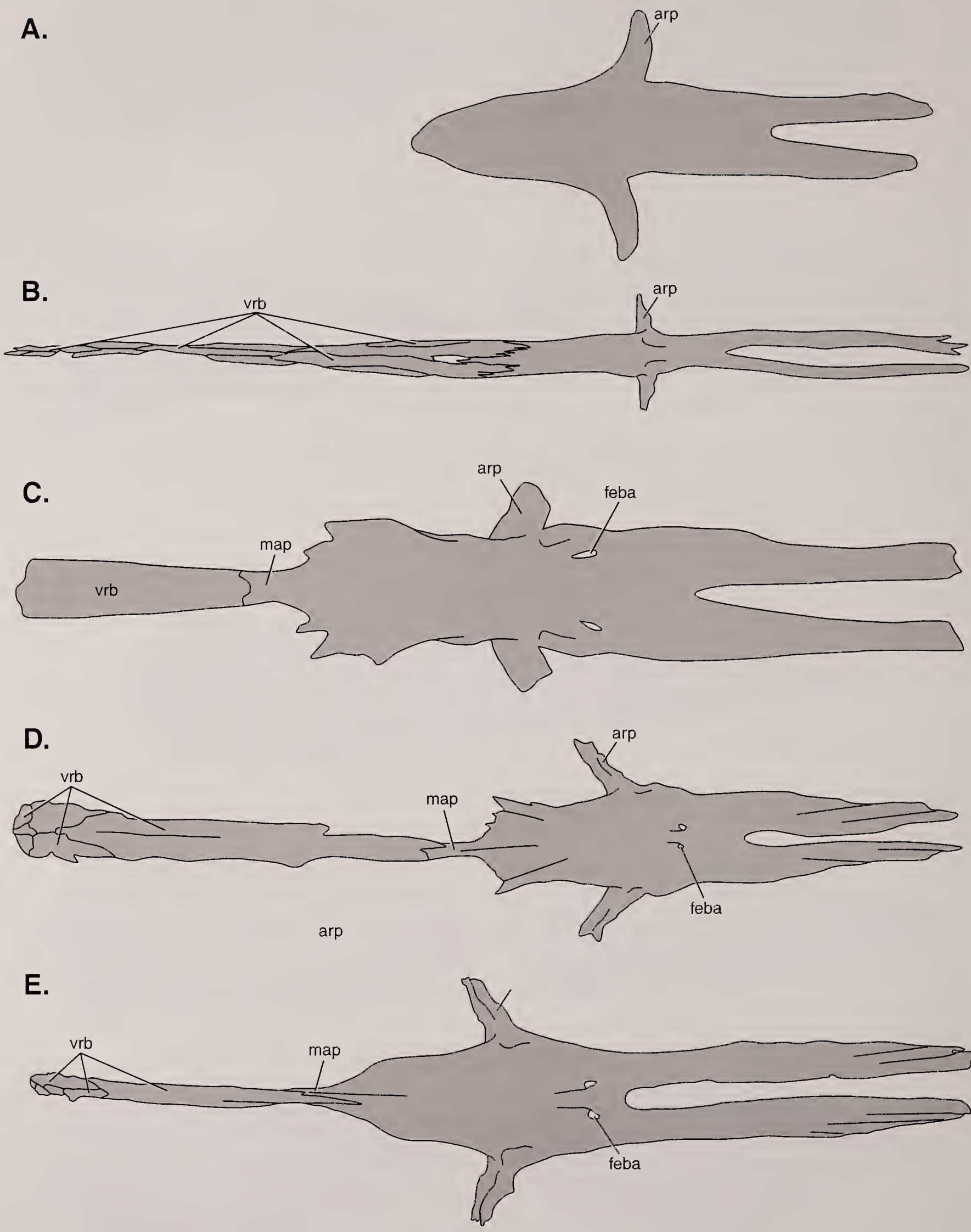


FIG. 132. Diagrammatic illustrations of the parasphenoid and ventral rostral bones of sturgeons and relatives. (**A**) †*Peipiaosteus pani* (after Grande & Bemis, 1996, fig. 6). (**B**) *Polyodon spathula* (after Grande & Bemis, 1991, fig. 6). (**C**) †*Priscosturion longipinnis* (after Grande & Hilton, 2006, fig. 18). (**D**) *Scaphirhynchus platorynchus* (FMNH 10324). (**E**) *Acipenser brevirostrum* (after Fig. 46). Abbreviations found on pages 8–9.

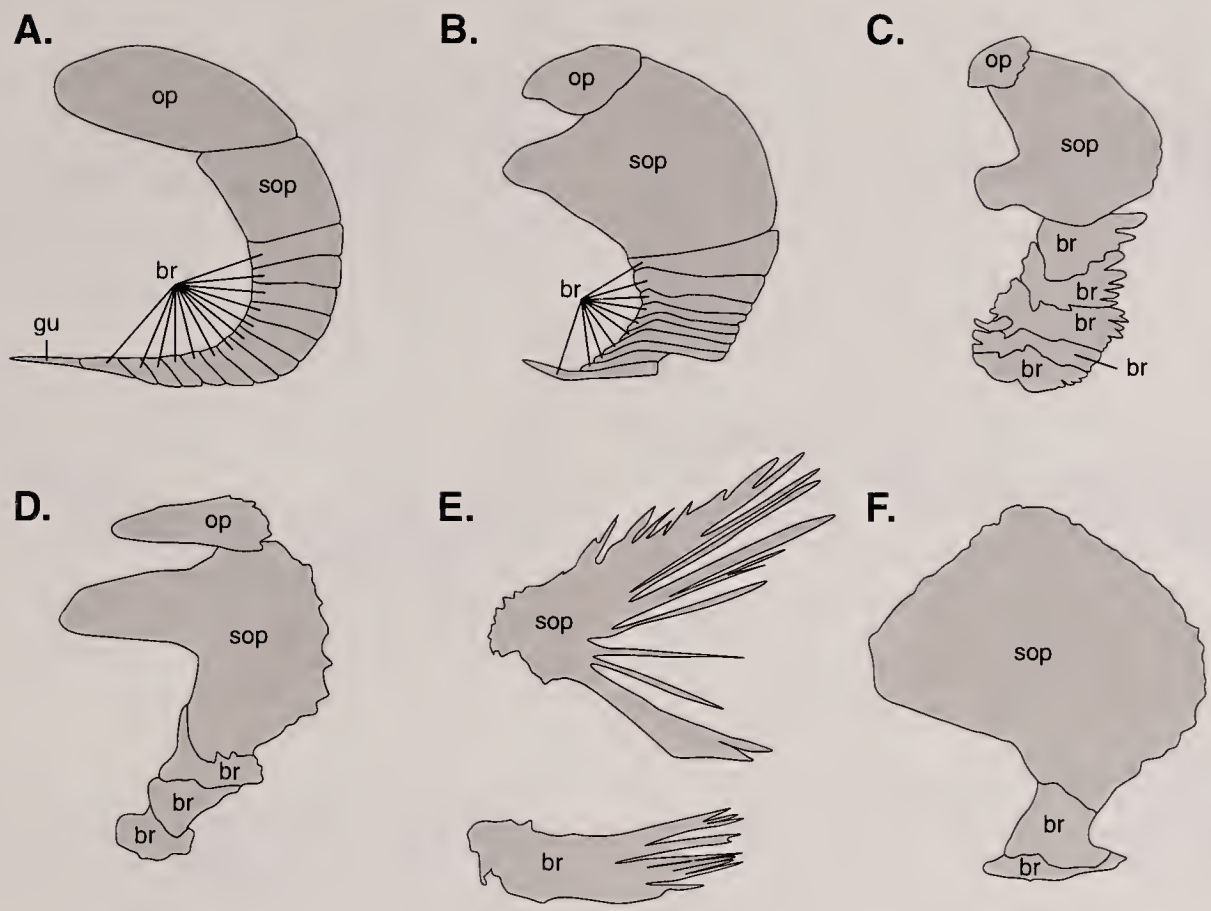


FIG. 133. Diagrammatic illustrations of the opercular series of sturgeons and relatives. (**A**) †*Moythomasia durgaringa* (after Gardiner, 1984, fig. 103). (**B**) †*Chondrosteus acipenseroides* (after Traquair, 1887, fig. 5). (**C**) †*Peipiaosteus pani* (after Grande & Bemis, 1996, fig. 8). (**D**) †*Protopsephurus liui* (after Grande et al., 2002, fig. 8). (**E**) *Polyodon spathula* (after Grande & Bemis, 1991, fig. 15). (**F**) *Acipenser brevirostrum* (after Fig. 26). Abbreviations found on pages 8–9.

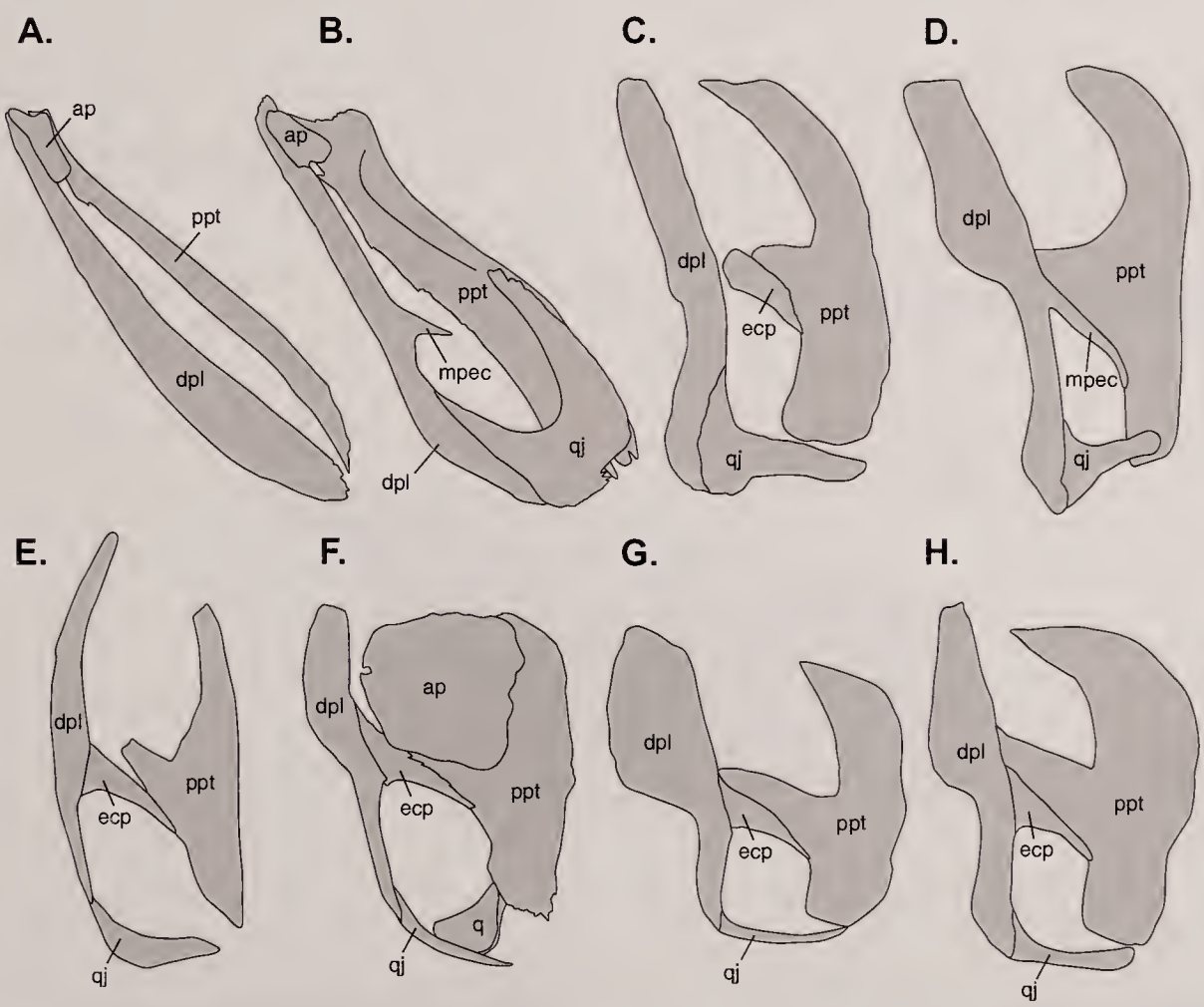


FIG. 134. Diagrammatic illustrations of the upper jaws of sturgeons and relatives. (**A**) *Polyodon spathula* (after Grande & Bemis, 1991, fig. 14). (**B**) *Psephurus gladius* (after Grande & Bemis, 1991, fig. 35). (**C**) †*Priscosturion longipinnis* (after Grande & Hilton, 2006, fig. 19). (**D**) *Huso huso* (CAS 211810). (**E**) *Scaphirhynchus platorynchus* (after Grande & Bemis, 1991, fig. 78G). (**F**) *Acipenser brevirostrum* (after Fig. 56). (**G**) *Acipenser baerii* (VIMS 12083). (**H**) *Acipenser transmontanus* (VIMS 12097). All are dorsal view except *Polyodon* (**A**) and *Psephurus* (**B**), which are lateral view; anterior to left in all. Ectopterygoid is ontogenetically fused to dermopalatine in *Scaphirhynchus* (Findeis, 1993); there is no evidence for an autogenous ectopterygoid in paddlefishes, although *Psephurus* (and all other paddlefishes except *Polyodon*) has an ectopterygoid process of the dermopalatine. Absence of an autopalatine in *Huso*, *Scaphirhynchus*, *A. baerii*, and *A. transmontanus* is likely an artifact of these specimens being of juvenile stages (i.e., the autopalatine has not yet ossified in these individuals); absence of autopalatine in †*Priscosturion* is due to lack of preservation (the autopalatine was preserved on other side of specimen). Abbreviations found on pages 8–9.

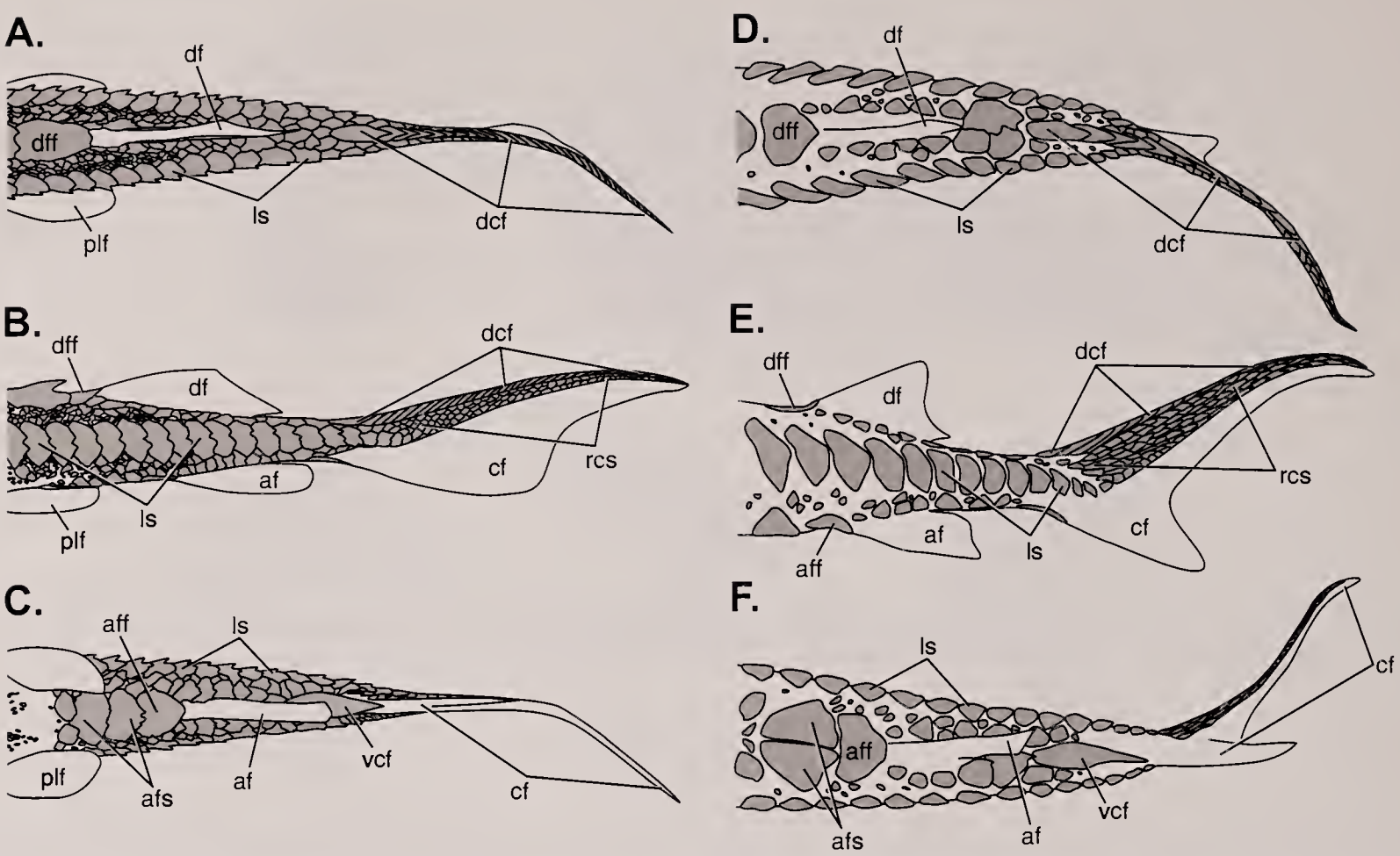


FIG. 135. Diagrammatic illustrations of the caudal peduncle armor. (**A**) Dorsal, (**B**) lateral, and (**C**) ventral views of *Pseudoscaphirhynchus hermanni* (uncataloged, currently housed at VIMS). (**D**) Dorsal, (**E**) lateral, and (**F**) ventral views of *Acipenser oxyrinchus* (VIMS uncataloged). Abbreviations found on pages 8–9.

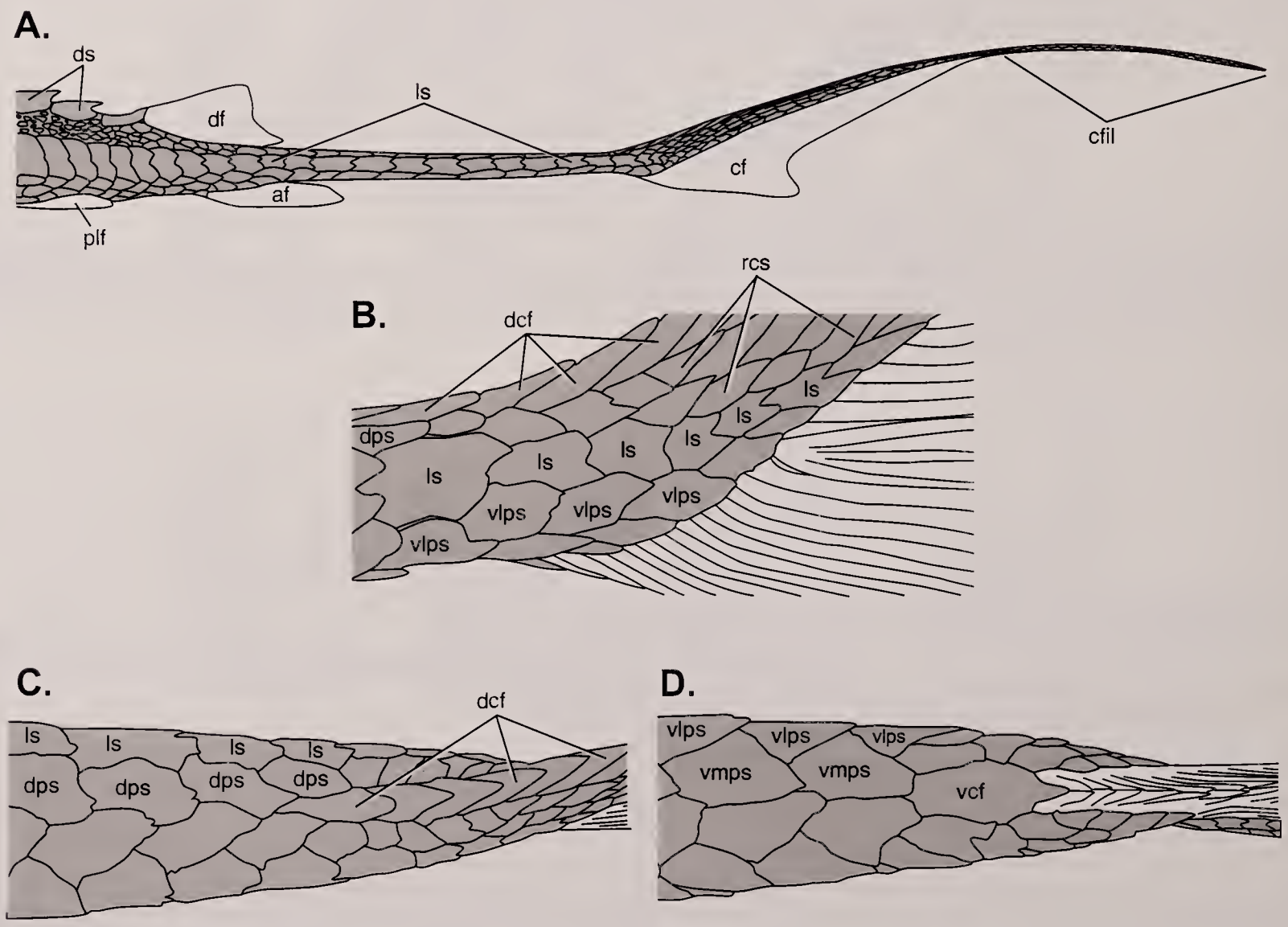


FIG. 136. Diagrammatic illustrations of the caudal peduncle armor of *Scaphirhynchus platorhynchus*. (**A**) Lateral view of entire caudal peduncle (VIMS 12098). (**B**) Lateral, (**C**) dorsal, and (**D**) ventral close-up views (after Hilton, 2004, fig. 3). Abbreviations found on pages 8–9.

we acknowledge that variation as well). The consistent difference that exists among taxa is in the ventral surface of the bone: whether this bone is flat or keeled. In both *Scaphirhynchus* and †*Priscosturion*, the posteriormost ventral rostral bone is completely flat and smooth along its entire length (e.g., see Grande & Hilton, 2006, figs. 11–16, for †*Priscosturion*). This differs from all other acipenserids examined (including *P. kaufmanni*), in which this bone is keeled. The posteriormost ventral rostral bone is also relatively much broader in †*Priscosturion* and *Scaphirhynchus* than in other acipenserids. For those taxa in which ventral rostral bones are absent, this character was coded as not applicable.

In the tree shown in Figure 128A, the condition of having a flat posteriormost ventral rostral bone is a synapomorphy of †*Priscosturion* + *Scaphirhynchus*, whereas in the other equally most-parsimonious topology (Fig. 128B), a flat posteriormost ventral rostral bone is a character of the family Acipenseridae, with a keel developing at the node above *Scaphirhynchus*.

Character 21. Surface of ventral rostral bones (0 = smooth, with only slight ornamentation; 1 = with a variable number of distinct prominences).

The ventral rostral bones of most polyodontids and acipenserids are typically smooth bones that have a keel (see the description of character 20 above); there may be slight ridges of ornamentation on their ventral surfaces. In *H. huso*, *A. ruthenus*, and *A. baerii*, we found a variable number of distinctly raised prominences on the ventral rostral bones. These are typically most fully developed and numerous on the more posterior elements of the series (e.g., the posteriormost bone or those immediately anterior to it). These protrusions are usually oval in shape and have a rough or ornamented ventral surface. The presence of these prominences is interpreted to be a synapomorphy of (*A. baerii* [*H. huso* + *A. ruthenus*]) on both topologies recovered in our analysis. For those taxa in which ventral rostral bones are absent, this character was coded as not applicable.

Character 22. Opercle (0 = larger than subopercle; 1 = smaller than subopercle; 2 = absent).

The homology of the opercular bones in acipenserids has been discussed by several authors (e.g., see Grande & Bemis, 1996; Bemis et al., 1997; Findeis, 1997). All extant acipenseriforms lack bones that correspond to the opercles of other actinopterygians. Fossil acipenseriform taxa do possess small opercles (e.g., †*Chondrosteus*, Hilton & Forey, 2009; †*Peipiaosteus*, Grande & Bemis, 1996; †*Protopsephurus*, Grande et al., 2002), although the subopercle is always the largest of the opercular series. Following Grande et al. (2002, character 1), we coded this as a multistate character. In both most-parsimonious cladograms, the presence of an opercle smaller than the subopercle supports Acipenseriformes, and the complete absence of the opercle supports the node Acipenseridae + Polyodontidae, with a reversal in †*Protopsephurus*. We regard this latter result as spurious and likely due to sparse taxon sampling within the family Polyodontidae: given the plesiomorphic position of †*Protopsephurus* within Polyodontidae (Grande et al., 2002), it is likely that the presence of a small opercle in this taxon is a retention of the plesiomorphic condition and that the loss of the opercle altogether occurred convergently in more derived polyodontids and in Acipenseridae.

Character 23. Branchiostegals (0 = elements grade smoothly in size and shape from dorsal to ventral; 1 = individual elements of distinctly different shapes).

Findeis (1997) discussed several variable aspects of the form of the branchiostegals of acipenserids, including shape, size, and number; we have divided the discussion of his character 7 (the presence or absence of a pair of branchiostegals) into several characters to capture this variation (our characters 23, 24, and 26). The branchiostegals of most basal actinopterygians, including †*Chondrosteus*, †*Peipiaosteus*, and polyodontids, form a series that grades in size and shape from the larger, more posterodorsal elements of the opercular series (e.g., the subopercle) to smaller elements anteroventrally (Fig. 133A–E). Although only a single branchiostegal element is present, *Polyodon* is coded as having this condition because the branchiostegal that is present maintains the pattern of being a smaller element that "fits" into the opercular series following the larger subopercle; Fig. 133E). In acipenserids, the branchiostegals (i.e., the elements of the opercular series ventral to the subopercle) show distinctly different shapes (Fig. 133F; see also Figs. 47–51), and there is no gradation between adjacent elements; this is resolved as a synapomorphy of the family Acipenseridae in our analysis. †*Priscosturion* is coded as unknown because only a single branchiostegal is preserved on either side; although the form of the element that is present closely resembles that of the dorsalmost branchiostegal of other acipenserids (see the discussion of character 26 below), we cannot be sure of the form of the more ventral elements if they existed.

Character 24. Branchiostegal number (0 = greater than seven; 1 = fewer than seven but greater than one; 2 = one).

Grande and Bemis (1996, characters D2, H2) defined two characters related to the reduction in number of branchiostegals in acipenseriform fishes; here we have combined these characters in to a single multistate character. Most basal actinopterygians have more than seven branchiostegals. Within the acipenseriform taxa surveyed here, only †*Chondrosteus* has more than seven (up to 11; Hilton & Forey, 2009; Fig. 133B); †*Peipiaosteus* has six or fewer branchiostegals (Grande & Bemis, 1996; Fig. 133D). Within polyodontids, there is variation: †*Protopsephurus* has three to four branchiostegals (Grande et al., 2002; Fig. 133D), whereas all other polyodontids have only a single branchiostegal (Grande & Bemis, 1991; Fig. 133E). All acipenserids typically have two branchiostegals, although there is intraspecific variation in the number and arrangement of the more ventral of these. †*Priscosturion* is coded as unknown because, although only a single branchiostegal is preserved on either side, this is likely because of a lack of preservation of the more ventral element(s). In our analysis, the presence of fewer than seven branchiostegals is a synapomorphy of the group (†*Peipiaosteus* [Polyodontidae + Acipenseridae]), with a further reduction to a single element in all polyodontids except †*Protopsephurus* (represented in our analysis by *Polyodon*).

Character 25. Posterior margin of the branchiostegals (0 = smooth; 1 = serrated).

Grande et al. (2002, character 18) coded this character and found the presence of a serrated posterior margin of the branchiostegal to independently occur in †*Peipiaosteus*

and in Acipenseridae + Polyodontidae. The degree of this serration is variable in those taxa in which it occurs (cf. Fig. 133C, E), although all taxa are distinct from those such as †*Chondrosteus* (Fig. 133B), in which the posterior margin of the branchiostegals is smooth. We coded †*Priscosturion* as unknown for the same reasons as characters 23 and 24. In all other members of Acipenseridae, the dorsalmost branchiostegal has a smooth posterior margin, whereas the more ventral element(s) have the same sort of serrated margins as found in †*Protopsephurus* (Fig. 133D; Grande et al., 2002). We agree with the coding of this character by Grande et al. (2002) but found it to be a synapomorphy of (†*Peipiaosteus* [Acipenseridae + Polyodontidae]).

Character 26. Dorsalmost branchiostegal pillar-like and laterally concave (0 = no; 1 = yes).

Findeis (1997, character 7, in part) noted that the dorsalmost branchiostegal of sturgeons "forms an elongate vertical support" between the subopercle and the more ventral branchiostegal(s), although there is variation in the overall shape of the branchiostegal (e.g., rectangular in *Acipenser*, *Huso*, and *Pseudoscaphirhynchus* and triangular in *Scaphirhynchus*; Findeis, 1997). The lateral surface of this branchiostegal, no matter what overall shape, is concave in all sturgeons. Grande and Hilton (2006, character 29) defined this as a distinct character in their analysis, which is followed here. The pillar-like, laterally concave condition was not found outside of Acipenseridae, and it is resolved as a synapomorphy of the family in our analysis.

Character 27. Anterior margin of subopercle (0 = rounded or lobate; 1 = with elongate anterior extension).

In his study, Findeis (1997, character 47) described various aspects of the shape of the subopercle in support of *Scaphirhynchus* + *Pseudoscaphirhynchus*, including the presence of a distinct anterior process and an elongate, dorsoventrally compressed form (Findeis also considered the condition in †*Protoscaphirhynchus* to be similar, citing Wilimovsky, 1956; however, the shape of the subopercle is unclear on the only known specimen of this taxon, and the element identified by Wilimovsky as the subopercle was reinterpreted as the clavicle by Hilton & Grande, 2006). We have slightly redefined this character.

We recorded this anterior extension in †*Priscosturion*, *Scaphirhynchus*, and *Pseudoscaphirhynchus*. Despite its similarity in these taxa, particularly in the extant genera as noted by Findeis, we did not find this character to support his "Scaphirhynchini." In our analysis, it is resolved as a character supporting †*Priscosturion* + *Scaphirhynchus* and independently found in *Pseudoscaphirhynchus* (Fig. 128A) or as a character at the base of Acipenseridae (†*Priscosturion* + extant acipenserids), with a reversal to a rounded anterior margin at the node above *Scaphirhynchus* and an independent evolution of the process in *Pseudoscaphirhynchus*.

Character 28. Posterior margin of subopercle (0 = smooth and rounded; 1 = serrated).

Grande et al. (2002, character 12) defined this as a multistate character, separating the weakly serrated condition of the posterior margin of the subopercle found in †*Protopsephurus* (Fig. 133D) from the strongly serrated condition found in other polyodontids (e.g., *Polyodon*; Fig. 133E). We collapsed both of these into a single "serrated" character state that was found to be a synapomorphy of Polyodontidae. The serrated condition is distinguished from the smooth and/or rounded condition found in other acipenseriforms and other basal actinopterygians (e.g., Fig. 133A–C, F). We will add the caveat, however, that the condition found in †*Protopsephurus* is far from that of other polyodontids and does bear some degree of similarity to the slightly scalloped condition found in some acipenserids.

Character 29. Palatal complex (0 = absent; 1 = present).

The cartilaginous palatal complex forms in the midline of the upper jaws posterior to the symphysis between the left and right palatoquadrates (see the discussion of character 30 below) and was considered by Findeis (1997, character 18) to be a synapomorphy of the family Acipenseridae, as was found in our analysis as well (coded as unknown in all fossil taxa because of a lack of preservation). There is substantial variation in the overall form of the palatal complex and its constituent cartilages, as was discussed by Findeis (e.g., in *Huso*, a large cartilage forms most of the surface area of the complex, whereas the total area is formed by a greater number of smaller cartilages in other acipenserids). There may be some systematic or taxonomic signal in this variation (e.g., Antoniu-Margoci, 1936a–d; Sokolov, 1989a,b), but it needs to be better studied and quantified (Findeis, 1997).

Character 30. Palatoquadrates (0 = without symphysis between *pars autopalatina*; 1 = with symphysis between *pars autopalatina*).

In most actinopterygians, the *pars autopalatina* region of the palatoquadrate articulates with the ethmoid region of the neurocranium, and the left and rights sides are separate. In Acipenseriformes, the left and right palatoquadrates meet in the midline, in the region that is considered to be *pars autopalatina*, representing a massive restructuring of the jaw elements in which the suspensorium is rotated (almost 90 degrees in acipenserids) from the "typical" actinopterygian condition. Grande and Bemis (1996, character B1, p. 105) noted that this is a "traditionally recognized character often cited as evidence of acipenseriform monophyly"; in our analysis, we found it to be a synapomorphy of Acipenseriformes. Although the *pars autopalatina* is largely cartilaginous in many taxa (the autopalatine is the last bone to ossify, and this region was found to be entirely cartilaginous in even large individuals of several taxa, e.g., *A. oxyrinchus*), the relative position of the other bones of the suspensorium (e.g., the dermopalatines and the palatopterygoids) allow this character to be coded for fossil taxa.

Character 31. Quadratojugal (0 = bridging palatoquadrate and dermopalatine; 1 = not bridging palatoquadrate and dermopalatine).

Grande and Bemis (1991, character 6) defined this character as "the presence of a triradiate bone [the quadratojugal] linking the palatoquadrate with the [dermopalatine]" and considered it to be a synapomorphy of Acipenseriformes, following Patterson (1982). We modified the definition of this character slightly, dropping reference to the variation in the shape of the quadratojugal (e.g., triradiate in acipenserids but

simple and elongate in †*Peipiaosteus*) while retaining the unique (relative to other basal actinopterygians) aspects of its position and relationship to other bones of the palatoquadrate. †*Boreosomus* and †*Birgeria* lack quadratojugals and therefore are coded as not applicable (Neilsen, 1949, mentions fragments of dermal bone that might be remnants of the quadratojugal in his specimens of †*Birgeria*, but this homology is uncertain). *Polyodon* is also coded as not applicable because it lacks a quadratojugal (Fig. 134A), although other polyodontids have a well-developed quadratojugal in a position similar to that of other acipenseriforms (Fig. 134B). In all taxa included in our analysis that could be scored for this character, the quadratojugal bridges the dermopalatine and palatoquadrate, and therefore our analysis is consistent with this as a synapomorphy of Acipenseriformes.

Character 32. Premaxillae and maxillae (0 = present; 1 = absent).

The identification of the bones that make up the dorsal oral jaws in Acipenseriformes has recently been discussed by Grande et al. (2002, p. 225), which we quote here (with omission of their figure references): "The upper jaw of †*Protopsephurus* [and other acipenseriforms] consists of two major bones: the palatopterygoid, and another bone termed maxilla in Grande and Bemis (1991) but later (Grande & Bemis, 1996; Bemis et al., 1997; and here) termed dermopalatine. Our interpretation of this bone as a dermopalatine is based on its pattern of development and its topographically close association with the palatatoquadrate (e.g., Bemis et al., 1997, fig. 18). Such studies show that, as in other actinopterygians, the dermopalatine of acipenseriforms forms in close association with the palatoquadrate cartilage, which it partially ensheathes. Were we to interpret this bone in the traditional way, as a maxilla, we then would be postulating not only that dermopalatines were lost phylogenetically in Acipenseriformes but also that the maxilla of Acipenseriformes secondarily evolved an unusually close contact with the surface of the palatoquadrate cartilage. In view of the available comparative anatomical and developmental data, it seems simpler to us to interpret this condition as resulting from only one change (loss of the maxilla), with the dermopalatines being retained in their plesiomorphic position as ensheathing elements of the palatoquadrate cartilage. This view is also consistent with the unquestioned absence of the premaxilla in acipenseriforms, an element that is primitively present in osteichthyans."

As noted above, the absence of these bones has been used in prior systematic analyses (e.g., Grande & Bemis, 1996, character B8; Grande et al., 2002, character 15) and found to be a synapomorphy of Acipenseriformes, as it was in our analysis.

Character 33. Ectopterygoid and dermopalatine (0 = separate; 1 = fused).

Findeis (1993) found that the ectopterygoid ontogenetically fuses to the dermopalatine in *Scaphirhynchus* and considered this to be a synapomorphy of the genus (Findeis, 1997, character 69). Findeis (1997, p. 116) noted that "in †*Paleopsephurus* (Grande & Bemis, 1991), an elongate process positionally similar to the acipenserid ectopterygoid is probably an independent bone ([his] Figure 22a), but the short process of *Psephurus* and *Polyodon* suggests that the ectopterygoid is lost in these genera." In contrast, we note that the resulting arrangement of this compound bone in *Scaphirhynchus* bears a striking resemblance to the dermopalatine of most polyodontids (e.g., †*Crossopholis*, Grande & Bemis, 1991, fig. 55; *Psephurus*, Grande & Bemis, 1991, fig. 35; Fig. 134B; †*Protopsephurus*, Grande et al., 2002, fig. 11), which bears a distinct ectopterygoid process (among polyodontids, only *Polyodon* lacks this process; Fig. 134A; in our matrix, *Polyodon* is coded as "N," as the ectopterygoid is absent as either a process of the dermopalatine or an autogenous element). In all polyodontids in which this process is present (including the extant *Psephurus*), its ontogeny is insufficiently known to determine if it is the product of a fusion, as in *Scaphirhynchus*, or if it represents a different condition. Nevertheless, we have chosen to code these two groups the same given their similar adult forms. A similar fusion is sometimes present in some specimens of *Acipenser*, although we regard the typical condition to be the two elements remaining separate. For instance, in some specimens of *A. fulvescens*, the two elements are completely fused (e.g., see Grande & Bemis, 1991, fig. 79, which shows the left palatoquadrate, and the ectopterygoid is labeled as the "ectopterygoid process of the maxilla," although on the right side of this specimen, the two elements are separate), while in others (e.g., FMNH 98256), the two elements remain separate. We found a fused dermopalatine and ectopterygoid to support the family Polyodontidae and genus *Scaphirhynchus*, indicating two independent gains of this condition.

Character 34. Medial dermopalatine expansion (0 = absent; 1 = slight medial broadening; 2 = greatly exaggerated medial broadening).

Findeis (1997, character 34) defined a broad medial portion of the dermopalatine to be the so-called dermopalatine shelf, and considered it to be a synapomorphy of his Acipenserinae (i.e., all acipenserids except *Huso*). Grande and Hilton (2006) described this character as a "bladelike ventral expansion on the anterior ventral edge of upper jaw." Whereas previous authors considered this character as a present–absent character, there is substantial variation in the development of the shelf (i.e., the degree of broadening of the medial portion of the dermopalatine). For instance, the expansion is only slightly developed in taxa such as *A. brevirostrum* (e.g., Fig. 134F), whereas in taxa such as *A. baerii* and *A. transmontanus* (Fig. 134G, H, respectively), the medial portion of the dermopalatine is greatly exaggerated. Further, we disagree that the shelf is absent in *Huso* but rather consider it only slightly developed (the slight expansion is not seen in Fig. 134E because of orientation of the specimen, but see Findeis, 1997, fig. 22b, in which this weakly developed broadening is visible for *Huso*). Therefore, we coded this as a multistate character.

Based on the two most-parsimonious topologies, two scenarios are possible: 1) a greatly exaggerated broadening occurs at the base of Acipenseridae, with independent evolution of a slight medial broadening supporting the clades *A. ruthenus* + *H. huso* and ([†*Priscosturion* + *Scaphirhynchus*][*A. brevirostrum* + *A. fulvescens*]) (Fig. 128A), or 2) a slightly broadened medial expansion arising at the base of Acipenseridae, with a change to a greatly exaggerated medial expansion in the clade (*A. oxyrinchus*, *A. transmontanus* ([*A. baerii* {*A. ruthenus* + *H.*

huso}]{*A. stellatus* + *Pseudoscaphirhynchus*}]), with a reversal in *A. ruthenus* + *H. huso* (Fig. 128B).

Character 35. Prearticular (0 = broad; 1 = small and thin; 2 = absent).

Findeis (1997, characters 35, 48) defined two characters related to the prearticular of acipenseriforms, one that distinguished the conditions found in, for instance, *Huso* and †*Crossopholis* (i.e., broad) from that of most acipenserids (i.e., thin) and one that defined the absence of a prearticular. Despite noting the "multiplicity of outgroup morphologies" (Findeis, 1997, p. 104), the former character was considered a synapomorphy of his Acipenserinae (= all acipenserids except *Huso*), and the latter was considered to be a synapomorphy of *Scaphirhynchus* + *Pseudoscaphirhynchus*.

In our analysis, we included both of Findeis's characters in a single multistate character. †*Birgeria* was coded as having a broad prearticular (see Nielsen, 1949, fig. 74), and †*Boreosomus* was coded as unknown (Nielsen, 1942, p. 342, makes some comments about the morphology of the prearticular in †*Boreosomus* but does not give any indication of its size, nor does he illustrate it, and he says that "the material is insufficient for so detailed a description" as he gave for †*Glaucolepis*). †*Chondrosteus* has a broad prearticular (Hilton & Forey, 2009), and this is the plesiomorphic condition for Acipenseriformes in both most-parsimonious cladograms from our analysis. On both topologies, a small, thin prearticular supports the node †*Peipiaosteus* + Acipenseroidei, with a loss of the prearticular occurring independently in †*Peipiaosteus*, *Scaphirhynchus*, and *Pseudoscaphirhyncus*, and with reversals to the plesiomorphic condition of having a broad prearticular in †*Protopsephurus* and *Huso*. Therefore, the presence of a small, thin prearticular was found to be not a synapomorphy of any subgrouping of Acipenseridae but rather plesiomorphic for the family. Because of the diversity of conditions found in other acipenseriforms (e.g., other polyodontids), this character should be reconsidered with a broader taxonomic sample of nonacipenserid acipenseriformes included.

Character 36. Posteroventral edge of hyomandibula (0 = does not flare; 1 = flares).

Two characters related to the shape of the posteroventral edge of the hyomandibula in acipenserids were defined by Findeis (1997, characters 19, 50). The first, the presence of a so-called dorsal posterior wedge was considered a synapomorphy of Acipenseridae (found in *Huso* and *Acipenser*), whereas a so-called ventral posterior wedge was considered a synapomorphy of *Scaphirhynchus* + *Pseudoscaphirhynchus* (see Findeis, 1997, fig. 11). These conditions were distinguished from that in polyodontids, in which the posteroventral edge of the hyomandibula is convex (these characters are difficult to consider in fossil taxa, as this portion of the hyomandibula in all extant acipenseriforms is cartilaginous; see below). We do not dispute the fact that there is variation within Acipenseridae in the shape of the hyomandibula (particularly in comparing *Scaphirhynchus* with other acipenserids). In our examination of *Pseudoscaphirhyncus hermanni*, we found a condition closer to that of *Acipenser* and *Huso* than to that of *Scaphirhynchus*, causing us to reconsider Findeis's character.

Our concept of this character is slightly different than that of Findeis (1997) in that we describe whether the ventral portion (largely cartilaginous) of the hyomandibula is flared. The ossified portion of the hyomandibula in all acipenseriformes (fossil and living) has a constricted midregion (i.e., is roughly hourglass shaped). In acipenserids, the distal end of the ossified region of the hyomandibula is much broader than the proximal end (that of †*Priscosturion* is only slightly broader, so to be conservative, we chose to code this character as unknown for this taxon). In †*Chondrosteus*, the hyomandibula appears to have been much more completely ossified than that of extant Acipenseriformes and generally looks like that of extant acipenserids, with a much broader distal end compared to the proximal end (Hilton & Forey, 2009); we therefore scored it the same as acipenserids. In †*Peipiaosteus* (Grande & Bemis, 1996, fig. 8) and fossil polyodontids (e.g., †*Crossopholis*, Grande & Bemis, 1991, fig. 54; †*Protopsephurus*, Grande et al., 2002, fig. 7), the ends of the ossified portion are roughly the same size, and it is unknown what shape the more distal cartilaginous region was in life. Although it is not unreasonable to assume that the cartilages were the same as in extant polyodontids, we code them as unknown for this character. The hyomandibula of †*Boreosomus* and †*Birgeria*, although of a completely different shape than that of Acipenseriformes, does not flare distally and therefore is coded as 0 for both taxa. Based on our analysis, we consider the distal flaring of the hyomandibula to be a character of Acipenseriformes, with a reversal in Polyodontidae.

Character 37. Interhyal–posterior ceratohyal articulation (0 = anteriorly positioned on interhyal; 1 = posteriorly positioned on interhyal).

As described by Findeis (1997, character 36), the articulation between the interhyal and the posterior ceratohyal is variable in its position within Acipenseridae. In *Huso* and *Polyodon*, this articulation is positioned anteriorly on the interhyal. In all acipenserids except *Huso*, this articulation is on the posterior half of the interhyal element (unknown in †*Priscosturion*). Findeis (1997) considered this to be a character of his Acipenserinae (all acipenserids minus *Huso*). However, in our analysis, we found the posterior position of this articulation to be a character of the family Acipenseridae, with a reversal occurring in *Huso*. This character could not be scored for any fossil taxa.

Character 38. Anterior shelf of hypobranchial 1 (0 = absent; 1 = present).

The first hypobranchial of members of Acipenseridae bears a distinct anterior shelf that covers the hypohyal and anterior portion of the anterior ceratohyal (e.g., see Fig. 72E, F). This character could not be scored for any fossil taxa. Findeis (1997) noted that "*Polyodon* possesses a small hypobranchial not comparable to other acipenseriform taxa." However, in that it lacks the shelf of acipenserids (e.g., see Grande & Bemis, 1991, fig. 17), we coded it as 0. Findeis (1997, character 21) found this to be a synapomorphy of the family Acipenseridae, as we did in our analysis.

Character 39. Median posterior branchial cartilage (0 = absent; 1 = present).

Findeis (1997, character 37) considered the absence of the so-called unidentified median cartilage that is positioned posterior to the basibranchial series in the ventral portion of

the gill arches of polyodontids (Grande & Bemis, 1991) to be a synapomorphy of all sturgeons except *Huso*, citing its absence in *Acipenser*, *Pseudoscaphirhynchus*, and *Scaphirhynchus*. However, we discovered this element in specimens of most species of *Acipenser* (all but *A. ruthenus*) and in both species of *Pseudoscaphirhynchus* that we examined. Therefore, in our analysis, absence of this cartilage appears to occur independently in *Scaphirhynchus* and some *Acipenser*. Because Findeis (1993) did not find this element in his exhaustive and detailed description of *Scaphirhynchus* and we did not find it in specimens available to us, we agree with him that the absence in this genus is real. However, this is a relatively small element that could easily be overlooked or lost during preparation if material is not carefully prepared, and we caution against scoring of this character based on small or poorly prepared specimens.

Character 40. Ossified basibranchials (0 = present; 1 = absent).

The basibranchial series of extant Acipenseriformes lacks any ossifications. In most fossil acipenseriforms (e.g., †*Peipiaosteus*, fossil polyodontids, and †*Priscosturion*), there are no bones preserved in the position of basibranchials. Although this may be due to preservation, other branchial arch elements are preserved in the available material, so we coded ossified basibranchials as absent in the taxa in our analyses. In contrast, an ossified basibranchial was discovered in †*Chondrosteus* by Hilton and Forey (2009, fig. 7), and these bones are known in both †*Boreosomus* and †*Birgeria* (Nielsen, 1942, 1949). Therefore, in our analysis, absence of ossified basibranchials was found to be a synapomorphy of †*Peipiaosteus* + Acipenseroidei.

Character 41. Gill rakers (0 = with teeth; 1 = without teeth).

The gill rakers of extant Acipenseriformes are variable in their overall shape, ranging from the short, stubby gill rakers of most acipenserids to the greatly elongated gill rakers of *Polyodon* that are used in filter feeding (see below for further comments on the variation of acipenserid gill rakers). In all extant acipenseriforms and most fossil acipenseriforms, the gill rakers lack denticles. This is in contrast to †*Chondrosteus* (Hilton & Forey, 2009) and most other basal actinopterygians, in which the gill rakers support denticles (†*Birgeria* and †*Boreosomus* are coded as unknown because the gill rakers in these taxa are not preserved; Nielsen, 1942, 1949). Absence of gill raker dentition is a synapomorphy of †*Peipiaosteus* + Acipenseroidei in our analysis.

Findeis (1997) defined two characters of the gill rakers within Acipenseridae. The first of these, the condition of having pronged gill rakers, he considered to be a synapomorphy of *Pseudoscaphirhynchus*. The second, having crenulated gill rakers, was found to be a synapomorphy of *Scaphirhynchus*. †*Chondrosteus* has relatively elongate, slightly curved gill rakers, whereas †*Peipiaosteus* (e.g., Grande & Bemis, 1996, fig. 6) and most other acipenserids (e.g., species of *Acipenser*; see Figs. 69, 70) have relatively short, triangular gill rakers. Findeis (1997, fig. 25) described the gill rakers of *Huso* as being elongate and similar in form to those of †*Chondrosteus* and basal polyodontids. However, they are not recurved, as in †*Chondrosteus*, and in our small cleared and stained specimen of *Huso*, they appear slightly longer than in comparably sized specimens of other taxa, but they are still triangular in overall shape. There is significant morphological variation of the gill rakers in acipenserids that requires further evaluation. However, there is substantial ontogenetic variation that also needs to be considered (e.g., in *A. brevirostrum*, the degree of "scalloping" appears to increase with size of the specimen). It is also unclear what the correlation is between the surface appearance of the soft tissue of the gill rakers and the form of the mineralized portion of the gill rakers. Therefore, both ontogenetic and taxonomic variation of the gill rakers of Acipenseridae needs to be studied further before it can be fully incorporated into a systematic analysis.

Character 42. Dorsal head of hyomandibula (0 = oval in cross section; 1 = circular in cross section).

Findeis (1997, p. 109, character 49) defined this character as follows: "The dorsal head of the hyomandibula of scaphirhynchines is cylindrical and ends in a small elliptical tip," which he differentiated from the "frontally expanded" dorsal head of all other extant acipenseriforms and considered to be a synapomorphy of *Scaphirhynchus* + *Pseudoscaphirhynchus*. We interpret that in this character, the "frontal expansion" results in the proximal end of the hyomandibula (both the ossified portion and the cartilaginous tip) being distinctly oval in cross section. Most acipenseriforms do have a broad proximal portion to the hyomandibula, which results in the ossified portion of the hyomandibula appearing to be "twisted" at its middle constriction (i.e., the long axis of the distal end is shifted 90 degrees relative to the long axis of the proximal end). On the other hand, the ossified portion of the hyomandibula of *Scaphirhynchus* is more or less circular in cross section (although the cartilage tip is more oval, as noted by Findeis). Both the ossified and the cartilaginous portions of the dorsal head of the hyomandibula in *Pseudoscaphirhynchus* are distinctly compressed and may be regarded as "frontally expanded" although admittedly not to the degree found in *Acipenser* and *Huso* (the condition in *Pseudoscaphirhynchus* is intermediate between the two extremes). Therefore, in our analysis, we found the condition of having a circular dorsal head to the hyomandibula to be a synapomorphy of the genus *Scaphirhynchus*.

Character 43. "Microctenoid" scales (0 = absent; 1 = present).

The trunk scales (denticular trunk scales of Grande & Bemis, 1991) of polyodontids are unique among acipenseriforms in that they are small and have a series of tooth-like posterior projections. These scales were referred to as "microctenoid" scales by Grande et al. (2002, character 4), who found their presence to be a synapomorphy of the family Polyodontidae, as was found in our analysis.

Character 44. Anterior abdominal scales (0 = present; 1 = absent).

Most basal actinopterygians have a scale jacket that covers the entire body. Within Acipenseriformes, the body squamation, although present in a variety of different forms (e.g., microctenoid scales of polyodontids, rhombic scales of †*Priscosturion*, and small isolated dermal elements in extant acipenserids), is greatly reduced, and interlocking scales are completely lacking from the anterior portion of the abdominal region. This was found by Grande and Hilton (2006, character 2) to be a synapomorphy of Acipenseriformes. In the present analysis, the absence of anterior abdominal scales was also observed in †*Birgeria*, and this character was found to be a

synapomorphy of †*Birgeria* + Acipenseriformes. The reduction of body squamation in †*Birgeria* has been noted before and used as evidence for a relationship with Acipenseriformes (e.g., Grande & Bemis, 1996, character A3; Bemis et al., 1997).

Character 45. Continuous series of median dorsal scutes extending from skull to dorsal fin (0 = absent; 1 = present).

Findeis (1997, character 1) and others have used the presence of five rows of scutes along the trunk as a synapomorphy of Acipenseridae (see also Grande & Bemis, 1996; Bemis et al., 1997). Grande and Hilton (2006) broke this character into the presence of median dorsal scutes, the presence of paired lateral scutes, and the presence of paired ventral scutes, following their description of †*Priscosturion*, which appears to lack ventral scutes but does possess the other three rows (i.e., the dorsal and paired lateral series are present). We also cite the developmental independence (i.e., different directionality and timing of development) among the different scute rows as justification for separating the "five-scute-rows" character.

Following Grande and Hilton (2006, character 15), we found the presence of a continuous series of dorsal scutes between the posterior margin of the skull and the anterior edge of the dorsal fin to be a synapomorphy of the family Acipenseridae. In †*Priscosturion*, these scutes are separate from (though adjacent to) the skull and posteriorly grade smoothly into the anterior dorsal fin rays. In most extant acipenserids, the anteriormost dorsal scute becomes incorporated into the skull roof through ontogeny (*Huso* is a notable exception), and posteriorly the dorsal scute series meets the large scute-like basal fulcrum at the anterior insertion of the dorsal fin, and they do not grade into the anterior fin rays.

Character 46. Trunk lateral line (0 = encased in normal interlocking scales; 1 = encased in slender tubes; 2 = encased in noninterlocking scales; 3 = encased in enlarged scutes).

As was the case with dorsal scutes (see the discussion of character 45 above), the presence of scutes positioned along the trunk lateral line of acipenserids is part of the character of five rows of body scutes that had traditionally been accepted as a synapomorphy of the family (e.g., Grande & Bemis, 1996; Bemis et al., 1997; Findeis, 1997). For the reasons given above, Grande and Hilton (2006) defined three characters related to the presence of each of the five rows (median dorsal, and paired lateral and ventral rows). Here we modify their character associated with the lateral row of scutes (their character 16) to capture the variation found in the form of the elements that surround the lateral line. This character is perhaps correlated with the reduction in body squamation.

Primitively in actinopterygians, the trunk lateral line is surrounded by scales that are similar in form to other body scales, here represented by †*Boreosomus*. In our analysis, the condition of having the trunk lateral line encased in slender tubes is a synapomorphy of †*Birgeria* + Acipenseriformes; in the basal acipenseriforms †*Peipiaosteus* (Grande & Bemis, 1996), †*Chondrosteus* (Hilton & Forey, 2009; also Hilton & Forey, unpubl., on specimens in the private collection of Mr. Chris Moore of Charmouth, England), and polyodontids (Grande & Bemis, 1991; Grande et al., 2002), the lateral line is surrounded by slender tubes. In the topology recovered in our analysis shown in Figure 128A, the presence of enlarged lateral scutes surrounding the lateral line was found to be a synapomorphy of the family Acipenseridae, with a subsequent change in †*Priscosturion*, which has the lateral line encased in thickened noninterlocking scales that differ in their overall form from the lateral scutes in extant acipenserids (see Grande & Hilton, 2006, fig. 28.1). Conversely, in the topology found in our analysis shown in Figure 128B, the presence of thickened noninterlocking scales is a synapomorphy of †*Priscosturion* + extant acipenserids, and then the presence of enlarged scutes along the lateral line is a synapomorphy of extant members of Acipenseridae.

Character 47. Ventral scute series (0 = absent; 1 = present).

The paired series of ventral scutes in acipenserids form free from association with any other structures (e.g., the dorsal scutes form in association with the dorsal fin fold, and the lateral scutes form in association with the lateral line sensory canal) and develop in both anterior and posterior directions from the midpoint of the series, and therefore were coded as a character distinct from other scute series by Grande and Hilton (2006). As was found by Grande and Hilton (2006, character 17), the presence of ventral scutes is unique to extant acipenserids and is a synapomorphy of all Acipenseridae except †*Priscosturion* on the topology of one of the equally most-parsimonious cladograms resulting from our analysis (Fig. 128B); the other most-parsimonious topology (Fig. 128A) resolves the presence of ventral scutes as a synapomorphy of all acipenserids, with a loss in †*Priscosturion*. Although this region is imperfectly known in the holotype and most complete skeleton of †*Priscosturion* (Grande & Hilton, 2002, fig. 4), the portions that are preserved show the body squamation of this taxon to be heaviest on the caudal peduncle and to grade to smaller, isolated scales anteroventrally on the body. The matrix that is preserved in this region shows no indication of any large bony plates as are found in extant sturgeons.

Character 48. Ossified supraneurals (0 = present throughout trunk; 1 = absent in subdorsal region and anterior caudal peduncle).

Grande and Bemis (1991) noted that ossified supraneurals in *Polyodon* and other polyodontids (e.g., †*Crossopholis*) form a continuous series along the entire vertebral column, although the subdorsal supraneurals are significantly smaller than the more anterior supraneurals. In other Acipenseriformes, the ossification of the supraneurals is interrupted below the dorsal fin and the anterior portion of the caudal peduncle. In Acipenseridae, the supraneurals (ossified or cartilaginous) disappear entirely ventral to the dorsal fin and for much of the length of the caudal peduncle (e.g., see Figs. 77, 78); for fossil acipenseriform taxa, it is unknown if cartilaginous supraneurals were present. In the polyodontid †*Protopsephurus*, the ossifications of the vertebral column are reduced, with only a few anterior neural spines present (Grande et al., 2002, fig. 5). Therefore, in our analysis, the presence of a completely ossified series of supraneurals is resolved as a synapomorphy of *Polyodon*, although it probably is a more inclusive character at a broader level within Polyodontidae.

Character 49. Caudal cercus (0 = absent; 1 = present).

Weisel (1978) described the anatomy of the cercus (= caudal fin filament) in *S. platorhynchus*. This structure, which is an

elongate posterior extension of the notochord posterior to the caudal fin (see Hilton, 2004), has traditionally been interpreted as a synapomorphy of *Scaphirhynchus* + *Pseudoscaphirhynchus* (e.g., Findeis, 1997, character 53). The caudal cercus can be well developed in *S. platorynchus* (see Fig. 115A), although it is typically broken in museum specimens and is best developed in small individuals; it is also present in the two other species of *Scaphirhynchus* (Mayden & Kuhajda, 1996). In *Pseudoscaphirhynchus*, the presence of the caudal cercus is taxonomically mosaic. The caudal cercus is well developed in *P. kaufmanni* (Fig. 115B). In *P. fedtschenkoi*, one morph possesses a caudal cercus, whereas the other does not. In *P. hermanni* (all morphs), the caudal cercus is absent.

In the tree shown in Figure 128A, the presence of a cercus is recovered as a character of †*Priscosturion* + *Scaphirhynchus* (unknown in †*Priscosturion*) and independently found in *P. kaufmanni*, whereas it was found to be present independently in *Scaphirhynchus* and *P. kaufmanni* in the other equally most-parsimonious topology (Fig. 128B).

Character 50. Caudal peduncle scutes (0 = absent; 1 = lateral line, postdorsal fin, postanal fin; 2 = lateral line, paired dorsal, paired ventrolateral, paired ventromedial; 3 = lateral, paired dorsal, large scutes intercalated between lateral series and ventral midline but not organized in distinct series).

Within Acipenseridae, there are varying degrees of armoring of the caudal peduncle (see Hilton, 2004, for general discussion). In *Huso* and all species of *Acipenser* examined here, the caudal peduncle armor consists of the lateral line scutes, which continue onto the caudal fin itself, as well as postdorsal fin and postanal fin scutes (see Figs. 106, 107, 135D–F). These scutes posterior to the dorsal and anal fins are typically large but are intraspecifically variable in their size, shape, and number in all species examined. Intercalated between the lateral line scutes and these postmedian fin scutes are other bony elements that range from small, isolated denticles to relatively large plates. However, even in taxa with large plates (e.g., *A. oxyrinchus*; Fig. 135D–F), there is "unarmored" skin between the various scutes. This differs from the condition found in *Pseudoscaphirhynchus*, in which the caudal peduncle is completely armored by irregularly arranged scutes of variable size and number that are positioned dorsal and ventral to the lateral line scutes (e.g., Fig. 135A–C). Anteriorly on the body, these scutes become much smaller and are similar to the interscute, denticular bony elements found in the skin of other acipenserids (Fig. 108). In *Scaphirhynchus* (Fig. 136) and †*Priscosturion* (Grande & Hilton, 2006, fig. 22), the caudal peduncle is also fully armored, although this is accomplished by organized series of scutes: the paired lateral line scutes, two pairs of ventrolateral scutes, and a single pair of dorsal peduncle scutes (Fig. 136). Findeis (1997, character 65) considered this complete armoring a synapomorphy of *Scaphirhynchus*. He did note a similar condition was present in †*Protoscaphirhynchus* but considered the single specimen to be too poorly preserved for accurate description. The specimen is indeed poorly preserved and prepared, and only the ventral portion is exposed; however, ventral lateral and ventral peduncle scutes are present (see Hilton & Grande, 2006, fig. 2).

The two topologies recovered as equally most-parsimonious cladograms in our analysis offer two different interpretations of the evolution of caudal peduncle armor in Acipenseridae. In the topology shown in Figure 128A, the condition found in *Acipenser* and *Huso* is interpreted as a synapomorphy of the family Acipenseridae, the condition found in †*Priscosturion* and *Scaphirhynchus* is a synapomorphy of those two genera, and the full armoring formed by disorganized scutes surrounding the lateral series was found to be a synapomorphy of the genus *Pseudoscaphirhynchus*. Conversely, in the topology shown in Figure 128B, the complete armoring of the type found in †*Priscosturion* and *Scaphirhynchus* was found to be a synapomorphy of the family Acipenseridae, and the absence of full caudal peduncle armoring (exemplified by *Huso* and *Acipenser*) was a synapomorphy of the genera *Huso*, *Acipenser*, and *Pseudoscaphirhynchus*, with a subsequent change in *Pseudoscaphirhynchus* to again having full armoring but of a different form than seen in †*Priscosturion* and *Scaphirhynchus*.

Character 51. Dorsal caudal fulcra (0 = one; 1 = more than one).

The dorsal margin of the caudal fin of most basal actinopterygians is lined by a series of dorsal caudal fulcra. Within Acipenseriformes, most taxa also have this series of elements, although there is significant variation in their overall form (e.g., between *Psephurus* and other acipenseriforms; see discussion by Hilton, 2004). The presence of only one dorsal caudal fulcrum was found to be an autapomorphy of †*Peipiaosteus pani* in both equally most-parsimonious cladograms in our analysis. However, within †Peipiaosteidae, there is perhaps the most significant variation in terms of number of dorsal caudal fulcra of any acipenseriform subgroup (see Grande & Bemis, 1996, character F1). As discussed by Grande and Bemis (1996) and Hilton (2004), the †peipiaosteids †*Yanosteus* and †*Spherosteus* both have a series of several dorsal caudal fulcra. In †*Stichopterus* and †*P. pani*, there is only a single dorsal caudal fulcrum (recovered in our analysis as an autapomorphy of †*P. pani*), and this was considered to be a synapomorphy of †*Stichopterus* + †*Peipiaosteus* by Grande and Bemis (1996). This character needs further evaluation, because of apparent intrageneric variation within †*Peipiaosteus*. Grande and Bemis (1996) considered †*P. fengningensis* to be conspecific with †*P. pani*. However, as shown by Jin (1999), †*P. fengningensis* clearly has several slender dorsal caudal fulcra (Hilton, 2004, suggested this could be a case of ontogenetic variation and that further study of the alpha taxonomy of †*Peipiaosteus* is needed).

Character 52. Ventral caudal fulcrum (0 = absent, 1 = present).

The presence of at least one ventral caudal fulcrum is widespread among basal actinopterygians. In most members of Acipenseriformes, there is a single, diamond-shaped ventral caudal fulcrum (e.g., Figs. 135, 136). Grande and Bemis (1996, character F2) considered the absence of a ventral caudal fulcrum to be a synapomorphy of †*Stichopterus* + †*Peipiaosteus*. Hilton (2004) cited Egerton (1858) and Davis (1887), as well as his own observations on a single specimen, in reporting the absence of a ventral caudal fulcrum in †*Chondrosteus* as well. However, in the study of Hilton and Forey (2009), a ventral caudal fulcrum was found in several specimens of †*C. acipenseroides*. Among out-groups, †*Birgeria* lacks a ventral caudal fulcrum (Nielsen, 1949). The absence of a ventral caudal fulcrum is homoplastic in †*Birgeria* and †*P. pani*.

Character 53. Pectoral fin spine (0 = absent; 1 = present).

The presence of a pectoral fin spine formed of dermal bone, the base of which becomes tightly associated with the propterygium, has traditionally been regarded as a synapomorphy of the family Acipenseridae (e.g., Findeis, 1997, character 2). However, pectoral fin spines occur within Acipenseriformes outside of Acipenseridae. Hilton and Forey (2009) found what they interpret to be a short pectoral fin spine in several specimens of †*C. acipenseroides*. Grande et al. (2002, character 22) described a pectoral fin spine in the basal polyodontid †*Protopsephurus* and noted also its presence in the †peipiaosteid †*Yanosteus*. Grande et al. (2002, p. 230) suggested that "the mere presence of a pectoral fin spine should no longer be used as a character of Acipenseridae, but its strong development into a long, stout element should be." See the section Pectoral Fin and Girdle above and Findeis (1993, 1997) for information on the development of the fin spine in members of Acipenseridae; the mode of development in fossil Acipenseriformes that also possess a fin spine (†*Chondrosteus*, †*Yanosteus*, †*Protopsephurus*, and †*Priscosturion*) is unknown but may be assumed to have been similar to that of extant members of Acipenseridae.

On both equally parsimonious topologies recovered in our analysis (Fig. 128), the presence of a pectoral fin spine supports Acipenseriformes, with independent losses in †*Peipiaosteus pani* and *Polyodon*. A taxonomically broader analysis, including more taxa outside of Acipenseridae, is needed before firm conclusions can be drawn, but we regard this scenario likely to stand, with †*P. pani* representing the loss of the fin spine in all †peipiaosteids except †*Yanosteus* and *Polyodon* representing the loss in polyodontids above the split between †*Protopsephurus* and all other polyodontids. We coded just the presence or absence of the spine and not any particular features of this element (although we do feel that the variation, e.g., relative strength, which is variable even within Acipenseridae [Findeis, 1997, p. 78], deserves further study).

Character 54. Supracleithrum reaching level of extrascapulars (0 = absent; 1 = present).

In nonacipenserid members of Acipenseriformes, the rigidity of the supracleithrum–posttemporal contact varies across taxa, but all have some degree of undercutting of the posttemporal by the supracleithrum (e.g., Grande & Bemis, 1991, figs. 13, 34; †*Peipiaosteus*, Grande & Bemis, 1996, fig. 5; polyodontids, Grande et al., 2002, fig. 8; †*Chondrosteus*, Hilton & Forey, 2009, fig. 7), although none are particularly tightly associated. This is in contrast to the condition found in members of Acipenseridae, in which the supracleithrum strongly undercuts the posttemporal by a well-developed anterior process. This portion of the supracleithrum was termed the "supracleithral shelf" and considered a synapomorphy of the family Acipenseridae by Findeis (1997, character 9). Because the supracleithrum undercuts the posttemporal in all Acipenseriformes, we distinguish the condition of acipenserids by noting that the anterior portion of the supracleithrum reaches anteriorly to the level of the extrascapulars in members of this family; this is a synapomorphy of Acipenseridae.

Character 55. Medial laminar expansion of cleithrum and clavicle forming rear of branchial (opercular) chamber (0 = absent; 1 = present).

Findeis (1997, character 10) considered the presence of median expansions of the cleithrum and clavicle that form the internal surface of the branchial chamber to be a synapomorphy of the family Acipenseridae. Since his analysis, additional material of several fossil acipenseriform taxa has been restudied, and it has been determined that †*Chondrosteus* (Hilton & Forey, 2009), †*Peipiaosteus* (Grande & Bemis, 1996), and some polyodontids (e.g., †*Protopsephurus*; Grande et al., 2002) also have this medial laminar wall of bone formed by both the cleithrum and clavicle (the level of contribution of the clavicle to this lamina is variable). In addition, the outgroups used here (†*Boreosomus*, Nielsen, 1942, fig. 75; †*Birgeria*, Nielsen, 1949, p. 269) also have a well-developed median expansion of the pectoral girdle (the clavicle of †*Boreosomus* is unknown, so it is not clear if this bone contributed to the laminar wall). Therefore, it is clear that this character is more widespread among basal actinopterygians. In most polyodontids, the dermal bones of the pectoral girdle are relatively slender, and there is no medial wall (see Grande & Bemis, 1991), and in our analysis, absence of this structure was found to be an autapomorphy of *Polyodon*.

Character 56. Cardiac shield (0 = absent; 1 = present).

The cardiac shield is a flat (*Scaphirhynchus*) or slightly rounded (*Pseudoscaphirhynchus*, *Huso*, and *Acipenser*) expansion of the cleithrum and clavicle. Findeis (1997, character 11) found this character to be a synapomorphy of the family Acipenseridae. Our analysis also recovered the presence of the cardiac shield as a synapomorphy of the family Acipenseridae (condition unknown in †*Boreosomus*).

Character 57. Posterior cleithral notch (0 = absent; 1 = present).

In lateral view, the posterior margin of the cleithrum of acipenserids bears a distinct notch (e.g., see Fig. 89 for the condition in *A. brevirostrum*, which is representative of the condition in extant acipenserids). Although in most regards the pectoral girdle of †*Priscosturion* is similar to that of extant acipenserids (e.g., presence of a pectoral fin spine, an enlarged supracleithrum that contacts the extrascapulars, and the presence of a cardiac shield), there is no distinct notch in the posterior margin of the pectoral girdle (e.g., Grande & Hilton, 2006, fig. 7). Grande and Hilton (2006, character 24) found this character to be a synapomorphy of the group comprising all extant sturgeons. In our analysis, we found the presence of this character to be a synapomorphy of either Acipenseridae with a reversal in †*Priscosturion* (Fig. 128A) or a synapomorphy of all acipenserids except †*Priscosturion* (i.e., all extant acipenserids; Fig. 128B).

This character is related to the so-called propterygium restraining process described by Findeis (1997, character 12; also a synapomorphy of Acipenseridae), which is a process that "extends from the lateral edge of the cleithrum ... to wrap anterolateral to the propterygial fossa of the scapulocoracoid ... and its articulating propterygium" (Findeis, 1997, p. 87). Findeis (1997, p. 87) also notes that this process is less prominent in *Huso* and *Acipenser* (than in the other extant genera), that it is best developed in juveniles, and that, when it is absent, "this region is enlarged as a robust cleithral notch

enfolding the base of the fin spine." Because of the ontogenetic and taxonomic variation in the presence of the process described by Findeis (1997), we prefer to code for the presence of the associated notch, which is observable at all ontogenetic stages.

Character 58. Clavicle and cleithrum suture (0 = absent or loose [not interdigitating]; 1 = present, tight and interdigitating).

Findeis (1997, character 13) described the interdigitation of the "clavicle process" and the cleithrum as a synapomorphy of the family Acipenseridae. We agree with this character, although we have redefined it slightly. In nonacipenserid acipenseriforms and in basal actinopterygians generally, the cleithrum and clavicle contact one another in a lap suture or only weakly contact one another at all (e.g., see Grande & Bemis, 1991, figs. 20, 42, 54, for varying degrees of contact between these bones in polyodontids). In acipenserids, the contact between the clavicle and the cleithrum is much more robust than in other acipenseriforms (e.g., see Fig. 88). In †*Priscosturion*, the clavicle and the cleithrum are sutured to one another though perhaps not quite as rigidly as in extant acipenserids (see Grande & Hilton, 2006, figs. 11–15). Still, because this taxon more closely resembles the condition in extant acipenserids than in, for instance, polyodontids, we coded this character as present and found it to be a synapomorphy of the family Acipenseridae.

Character 59. Supracleithral cartilage (0 = absent; 1 = present).

The supracleithral cartilage is a small, independent cartilage associated with the medial face of the supracleithrum in members of Acipenseridae (e.g., see Fig. 90). Findeis (1997, character 15) defined this character and considered it to be a synapomorphy of Acipenseridae, as did we. Because this structure is entirely cartilaginous, it was coded as unknown in all fossil taxa included in our analysis.

Character 60. Round-based scales (0 = absent; 1 = present).

Round-based scales are those scales that form on the pectoral girdle of acipenseriforms and are particularly well developed on the cleithral and clavicular laminae that form the posterior wall of the branchial chamber. Findeis (1997, character 23) distinguished the acipenserid round-based scales from those of polyodontids (see Grande & Bemis, 1991) based on the number of posterior extensions present on each scale (one in polyodontids and more than one in acipenserids). However, we are impressed with the overall similarity of these structures (cf. Fig. 94 with Grande & Bemis, 1991, figs. 23B, 45B, 63D) and consider them homologous across taxa and code the presence or absence of this form of scale (despite possible variation in number of posterior extensions, which are individually variable; see Fig. 94). These round-based scales are present in †*Peipiaosteus pani* (Grande & Bemis, 1996), polyodontids (Grande & Bemis, 1991), and most acipenserids (e.g., Findeis, 1997; present study). These scales are absent in †*Chondrosteus* (Hilton & Forey, 2009). Among polyodontids, †*Protopsephurus* lacks these scales; although this may be due to lack of preservation (Grande et al., 2002), we coded this absence as "real" because numerous other delicate structures are preserved on the specimens described and illustrated by Grande et al. (2002), and therefore we would expect these structures to be preserved if they were indeed present. We coded †*Priscosturion* as lacking round-based scales for similar reasons as †*Protopsephurus*. Among extant acipenserids, only members of the genera *Scaphirhynchus* and *Pseudoscaphirhynchus* lack these scales, and this absence was considered a synapomorphy of the two genera by Findeis (1997, character 54).

In our analysis, the two equally most-parsimonious cladograms suggest different evolutionary histories of the round-based scales. The topology shown in Figure 128A suggests that the presence of round-based scales supports the node †*Peipiaosteus* + Acipenseroidei, with independent losses in †*Protopsephurus*, †*Priscosturion* + *Scaphirhynchus*, and *Pseudoscaphirhynchus*. Conversely, the topology in Figure 128B suggests that round-based scales independently evolved in †*Peipiaosteus*, *Polyodon*, and the group comprising all acipenserids except †*Priscosturion* and *Scaphirhynchus*, with a subsequent loss in *Pseudoscaphirhynchus*.

Character 61. Clavicles (0 = not sutured; 1 = sutured).

The left and right clavicles of acipenseriforms may approach the midline but remain free from one another (e.g., †*Chondrosteus*, Hilton & Forey, 2009; †*Peipiaosteus*, Grande & Bemis, 1996; most polyodontids, Grande & Bemis, 1991, Grande et al., 2002) or suture to one another (*Polyodon*; Grande & Bemis, 1991; Acipenseridae in the present study). This character was found to be a character of Acipenseroidei with a reversal in †*Protopsephurus*. However, this is likely a function of taxon sampling within Polyodontidae, as in most polyodontids the left and right clavicles are not sutured together but rather are only loosely contact one another, if at all (Grande & Bemis, 1991).

Character 62. Anterior junction of clavicles (0 = convex; 1 = straight line).

Findeis (1997, character 59) defined a similar character to this one as a synapomorphy of *Pseudoscaphirhynchus* and phrased it as the "clavicle tips meet as an anteromedial wedge." However, our interpretation of the morphology of this region differs slightly. In all acipenserids, in ventral view there is a pair of anterolateral processes, one each on the left and right clavicle. In between these processes (i.e., the region in which the clavicle meets its antimere), the left and right clavicles extend forward to a varying degree, forming a convex margin. This convex margin is most exaggerated in *Pseudoscaphirhynchus* (Findeis's "wedge"; Findeis, 1997, fig. 26c) but can be recognized as being slightly developed in other acipenserids (e.g., Findeis, 1997, fig. 26a, b); the degree of the anterior extension is widely variable, and the left and right sides may instead form an irregular margin (e.g., Fig. 38). In *Scaphirhynchus*, on the other hand, the left and right clavicles stereotypically meet each other in a perfectly straight line (e.g., Grande & Bemis, 1991, fig. 78E). Such a condition is not seen elsewhere in Acipenseriformes or among other basal actinopterygians. This character was coded as not applicable for most fossil taxa included in this analysis because the left and right clavicles do not suture together (e.g., †*Birgeria*, †*Chondrosteus*, †*Peipiaosteus*, and †*Protopsephurus*). The details of the relationship between the left and right clavicles are unknown in †*Priscosturion* (Grande & Hilton, 2006, figs. 11–15, 27), and therefore this taxon was coded as unknown. In our analysis, the presence of a straight-line junction between the left and right

clavicles was found to be either a synapomorphy of †*Priscosturion* + *Scaphirhynchus* (again, unknown in †*Priscosturion*) (Fig. 128A) or a synapomorphy of *Scaphirhynchus* (Fig. 128B).

Conclusions

> *There is but little to justify the too common attitude that the possibilities of morphology are exhausted. Much disconnected fragmentary work has been done, but how little is known about the evolution of any one system of organs; how very few animals, if indeed there are any, whose structure, development, and paleontological record are known with even approximate fullness or accuracy.*
>
> —W. Patten (1912, p. vi)

Paraphyly of *Acipenser* and the Importance of Classification

While basic and applied aspects of biological sciences (e.g., phylogenetics and fisheries science, respectively) are often considered distinct disciplines, they are better viewed as different points along a continuum and have much to offer one another through interchange of data. Taxonomy and classification are essential tools for communication of biological data, and these classifications must convey the phylogenetic history of a group so that generalization of known information may be extended to taxa for which data is currently unknown or inaccessible; the classification may then be considered "predictive" (Cracraft, 2002). Beyond their specific results, which inform about the phylogenetic history of a particular group of organisms and can be used to understand its evolutionary history, systematic studies also provide a framework in which other types of biological data can be interpreted.

Because they are culturally and economically important (e.g., as the source of caviar), there is strong general interest in sturgeon biology in both scientific and public circles (e.g., Saffron, 2002; Carey, 2005). These long-lived, highly migratory fishes have been heavily impacted by human activities, and most are endangered or threatened (e.g., see CITES, http://www.cites.org). A significant amount of important research has been conducted on these fishes from ecological, behavioral, and conservation perspectives, although many questions remain to be addressed (Birstein, 1993; Billard and Lecointre, 2001). As shown by our results, there are also significant gaps in our understanding of evolution of these fishes. Sturgeons, therefore, offer a good example of the applied importance for evolutionary studies. With specific reference to systematic ichthyology and fisheries science, Collette and Vecchione (1995) outlined five ways in which this interchange of data can take place, including the systematic identification of management units (stocks and species), fisheries surveys as a source for materials for systematic studies, the use of monitoring data for biological inventories, the consideration of phylogeny in making management decisions (particularly using well-studied taxa as models for poorly known but closely related taxa), and the value of archived biological collections as resources for addressing fisheries-related problems.

As a group, sturgeons exemplify each of these relationships between basic and applied aspects of the biology of fishes. Here we offer admittedly brief examples of such data interchange (using Collette and Vecchione's five themes as an outline) that is possible from the study of sturgeons:

- Because of their life history (i.e., highly migratory but relatively faithful to specific rivers or drainages for spawning), species of sturgeons often have significant phylogeographic patterns, and this patterning is often the basis of proposed management units (e.g., the proposed five distinct population segments for *A. oxyrinchus* along the east coast of the United States; Atlantic Sturgeon Status Review Team, 2007).
- The present morphological study of *A. brevirostrum* was based almost exclusively on specimens collected as incidental mortalities for ongoing ecological and population monitoring surveys, and the developmental series used here was collected in association with series reared for studies aimed at better understanding the ontogeny of behavior in early life history stages of sturgeons. Such cooperative efforts continue to expand the comparative specimen base for the ongoing sturgeon research program by the first author and his colleagues.
- While one-time collections (often the case for collections made specifically for materials for systematic studies) are critical for faunal or regional studies, the regular, long-term surveys made for fisheries biology purposes provide vital data for distributional studies. Specifically, multispecies surveys provide significant data on the temporal and geographic distributions of species. Unfortunately, much of these data remain in gray literature that is not typically available to or used by the systematic ichthyological community for biogeographic or other evolutionary analyses, in part often because of lack of peer review (Collette, 1990). Sturgeon catches from fisheries surveys provide records, specimens, and, if tissues are taken and genetic analyses made, indication of migratory habits, for instance, that can then be incorporated into systematically based analyses of stock structure, which can in turn be incorporated into management plans.
- Poorly known taxa are often the most critically endangered or for other reasons not available for direct and intensive ecological or populational studies. With an understanding of phylogeny, better-known taxa that are close relatives may be used as proxies for the poorly known taxa. For example, the three species of the Aral Sea genus *Pseudoscaphirhynchus*, all of which are endangered (with *P. fedtschenkoi* possibly extinct), have always been regarded as most closely related to the North American genus *Scaphirhynchus* and therefore regarded as a "scaphirhynchin"-type sturgeon. However, following from the results of recent phylogenetic studies that the genus *Pseudoscaphirhynchus* is most closely related to the Ponto-Caspian species *A. stellatus*, *Scaphirhynchus* may not be an appropriate "comparison taxon" for *Pseudoscaphirhynchus*, and *A. stellatus* may better serve this role. It should be emphasized, however, that given known behavioral and ecological variation even within species of sturgeon, such extrapolation should be done with caution.
- The continuing and critical value of collections to state-of-the-art biological organismal science cannot be understated. This is particularly relevant to studies of sturgeon biology. Sturgeons present numerous curatorial challenges (e.g., large

adult body size of many species preventing preservation of complete specimens), and these challenges have limited holdings of many species to very small individuals and juvenile specimens. We were struck by the relative paucity of specimens for many species of sturgeons and the inadequacy of many specimens to accurately code similar life history stages (e.g., "adult condition"). This has limited the phylogenetic inferences that we have been able to make in the current study and presents challenges to overcome in future studies of sturgeon evolution.

Although, as noted above, there are limitations to the understanding of the phylogeny of sturgeons, it can be confidently said that the current classification of extant members of Acipenseridae does not reflect the phylogenetic relationships within the family as they are currently understood. For example, the fact that *Acipenser*, the most species-rich genus of sturgeons, is paraphyletic is now well established, using both morphological and molecular data (Bemis et al., 1997; Findeis, 1997; Birstein et al., 2002; Dillman et al., 2007; Krieger et al., 2008; present study). Recent analyses suggest that *Huso* is also not monophyletic (Birstein & DeSalle, 1998; Zhang et al., 2000; Ludwig et al., 2001; Birstein et al., 2002; Krieger et al. 2008; Vasil'eva et al., 2009), with both species being included in the genus "*Acipenser*" by Vasil'eva et al. (2009). The modern taxonomic conceptualization of the family (i.e., the classification of species in four genera) has been used for over 100 years (Berg, 1904), although more than 20 names have been used as genus-group names (Eschmeyer & Fricke, 2008; many of these names, however, are not available for a variety of reasons). The alpha taxonomy of sturgeons is even more extensive, with hundreds of names in the literature for the 25 currently recognized extant species (Table 9). Yet, as Dillman et al. (2007, p. 295) concluded, the "taxonomy of sturgeon species should not be altered on the basis of any single data set ... [and] we do not feel that the data sets assembled to date provide sufficient resolving power to alter any currently recognized genera." The present study is the first critical treatment of species-level morphological variation within sturgeons and aimed to begin the process of taxonomic revision by working from published data and original observations to establish a morphological baseline that can grow to become a taxonomically comprehensive data set. Our data can be then added and compared to new morphological data—as well as to published and new molecular character data—for a critical and robust analysis of sturgeon evolution. A predictive classification of Acipenseridae will be particularly valuable for conservation efforts of sturgeons and will be possible only through the sort of detailed phylogenetic study attempted above that is expanded to include *all* species, fossil and living, from both morphological and molecular perspectives.

Classification of Acipenseridae

Although a full revisionary taxonomic analysis of the family Acipenseridae is not possible at this time because of a lack of adequate specimens for several species of Acipenseridae (in particular some members of *Acipenser*), we offer a provisional classification based on the result of our phylogenetic analysis. We alter the usage of the subfamily Husinae Findeis, 1997, to include *A. ruthenus* (in addition to *Huso*) and propose the new subfamily Pseudoscaphirhynchinae (to include *Pseudoscaphirhynchus* and *A. stellatus*) because both groups have been also recovered through analysis of other data sets as well (e.g., molecular data of Birstein et al., 2002, and Dillman et al., 2007; morphological data of the current study). However, we refrain from making any genus-level modifications to the taxonomy of sturgeons until a rigorous analysis including all species of sturgeons can be performed.

In the following classification, we have placed the genus name *Acipenser* in quotation marks, following standard convention for when the monophyly of a taxon cannot be demonstrated (see Wiley, 1981; Grande & Bemis, 1998, p. 18). We have refrained from using quotation marks for *Acipenser* throughout the manuscript, however, for two reasons. First, because the paraphyly of *Acipenser* is not a particularly new or controversial result and it is alluded to throughout the manuscript, we feel that the repetitive use of "*Acipenser*," given the prevalence of the name in the text, would be unnecessarily distracting with little benefit. Second, because of the limitations of specimens and detailed comparative data, we have not been able to resolve the taxonomy of sturgeons (i.e., to diagnose species of the family into monophyletic groups that can be recognized as genera) and therefore do not see value in changing the common usage of *Acipenser* until such groups of sturgeon can be rigorously defined. However, the use of quotation marks in this formal classification does have value in that it points to the problematic level in forming a predictive classification of Acipenseridae. Said in another, perhaps overly vernacular way, although we want to make the point that *Acipenser* is paraphyletic, until something can be done about diagnosing monophyletic genera within Acipenseridae, it is better to leave the current usage alone in the spirit of taxonomic consistency (even the slight change from *Acipenser* to "*Acipenser*" is likely to cause undue confusion both within the systematic ichthyology community and within management and legislative realms).

Order Acipenseriformes Berg, 1940
- Suborder †Chondrosteoidei *sensu* Grande and Bemis, 1991
- Suborder †Peipiaosteoidei *sensu* Grande and Bemis, 1996
- Suborder Acipenseroidei *sensu* Grande and Bemis, 1991
  - Family Polyodontidae Bonaparte, 1838
  - Family Acipenseridae Bonaparte, 1831
    - Plesion †*Protoscaphirhynchus* Wilimovsky, 1956, *insertae sedis*
    - Plesion †*Priscosturion* Grande and Hilton, 2009, *sedis mutabilis*
    - Genus *Scaphirhynchus* Heckel, 1836, *sedis mutabilis*
    - Genus "*Acipenser*" Linnaeus, 1758
    - Subfamily Husinae Findeis, 1997 (new usage), *sedis mutabilis*
      - Genus *Huso* Linnaeus, 1758
      - "*Acipenser*" *ruthenus* Linnaeus, 1758
    - **Subfamily Pseudoscaphirhynchinae new subfamily, *sedis mutabilis***
      - Genus *Pseudoscaphirhynchus* Nikolskii, 1900
      - "*Acipenser*" *stellatus* Pallas, 1771

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University of Massachusetts, Amherst, and it became a primary research project for E.J.H. in 2002 when he became a postdoctoral research scientist at FMNH and was completed after he began his position at VIMS in 2007. This study would not have been possible without the support and generous donation of specimens of *Acipenser brevirostrum* by Boyd Kynard, Erika Henyey-Parker, and Micah Kieffer (collected and raised under Endangered Species Permits to Kynard). For more than 10 years, Micah Kieffer and Boyd Kynard retained the gill net mortality specimens that they donated to us and that formed the basis of much of this study. As a technician and graduate student working with Kynard, Alan Richmond raised the *A. brevirostrum* embryos (in the early and middle 1980s) that we examined and served as the starting point for our study of the skeletal ontogeny of *A. brevirostrum*. More recently, Erika Henyey-Parker, again as a student with Kynard, raised and collected most of specimens of the early life history stages used in this study. We thank all these people for making available these specimens that were so important to our study, for their constant support and interest in our research, and for their commitment and all that they have done to promote and advance the understanding of sturgeon biology in all its facets.

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Appendix I

Characters Used in Analysis

Below we provide a list of the characters used in our systematic analysis. For further explanation of these characters and their coding, refer to the text.

Character 1. Well-developed anterior and posterior divisions of the *fenestra longitudinalis* (0 = absent; 1 = present)
Character 2. Frontal bones (0 = separated in midline; 1 = meet in midline)
Character 3. Parietals (0 = ending anterior to posttemporals; 1 = extending posterior to posttemporals)
Character 4. Stellate bones (0 = absent; 1 = present)
Character 5. Jugal bone (0 = distinct horizontal and vertical arms [reverse-L shaped]; 1 = horizontal and vertical arms not distinct [triangular])
Character 6. Postorbital bone (0 = present; 1 = absent)
Character 7. Horizontal arm of jugal bone (0 = does not reach nasal capsule; 1 = undercuts nasal capsule)
Character 8. Medial process of jugal (0 = present; 1 = absent)
Character 9. Supraorbital bone (0 = absent; 1 = present without a descending process; 2 = present with a wedge-shaped descending process; 3 = present with a greatly expanded descending process)
Character 10. Median extrascapular (0 = absent; 1 = present)
Character 11. Rostral canal (0 = straight; 1 = curved)
Character 12. Dorsal rostral bone shape (0 = elongate and narrow; 1 = short and broad)
Character 13. Spines on dermal skull bones (0 = absent; 1 = present)
Character 14. Trunk, occipital, supraorbital lateral lines (0 = meet in posttemporal; 1 = meet in lateral extrascapular)
Character 15. Posterior elongation of parasphenoid (0 = absent; 1 = present)
Character 16. Ascending process of parasphenoid (0 = extends perpendicularly; 1 = extends anteriorly; 2 = extends posteriorly)
Character 17. Median anterior process of the parasphenoid (0 = absent; 1 = present)
Character 18. Ventral rostral bones (0 = absent; 1 = present)
Character 19. Posteriormost ventral rostral bone (0 = paired; 1 = single)
Character 20. Posteriormost ventral rostral bone (0 = keeled; 1 = flat)

Character 21. Ventral rostral bones (0 = with only slight ornamentation; 1 = with a variable number of distinct prominences)
Character 22. Opercle (0 = larger than subopercle; 1 = smaller than subopercle; 2 = absent)
Character 23. Branchiostegals. (0 = grade smoothly in size and shape from dorsal to ventral; 1 = of different shapes)
Character 24. Branchiostegal number (0 = greater than seven; 1 = fewer than seven but greater than one; 2 = one)
Character 25. Posterior margin of the branchiostegals (0 = smooth; 1 = serrated)
Character 26. Dorsalmost branchiostegal pillar-like and laterally concave (0 = no; 1 = yes)
Character 27. Anterior margin of subopercle (0 = rounded or lobate; 1 = elongate anterior extension)
Character 28. Posterior margin of subopercle (0 = smooth and rounded; 1 = serrated)
Character 29. Palatal complex (0 = absent; 1 = present)
Character 30. Palatoquadrates (0 = without symphysis between *pars autopalatina*; 1 = with symphysis between *pars autopalatina*)
Character 31. Quadratojugal (0 = bridging palatoquadrate and dermopalatine; 1 = not bridging palatoquadrate and dermopalatine)
Character 32. Premaxillary and maxillary bones (0 = present; 1 = absent)
Character 33. Ectopterygoid and dermopalatine (0 = separate; 1 = fused)
Character 34. Medial dermopalatine expansion (0 = absent; 1 = slight medial broadening; 2 = greatly exaggerated medial broadening)
Character 35. Prearticular (0 = broad; 1 = small and thin; 2 = absent)
Character 36. Posteroventral edge of hyomandibula (0 = does not flare; 1 = flares)
Character 37. Interhyal-posterior ceratohyal articulation (0 = anterior on interhyal; 1 = posterior on interhyal)
Character 38. Anterior shelf of hypobranchial 1 (0 = absent; 1 = present)
Character 39. Median posterior branchial cartilage (0 = absent; 1 = present)
Character 40. Ossified basibranchials (0 = present; 1 = absent)
Character 41. Gill rakers (0 = with teeth; 1 = without teeth)
Character 42. Dorsal head of hyomandibula (0 = oval in cross section; 1 = circular in cross section)
Character 43. "Microctenoid" scales (0 = absent; 1 = present)
Character 44. Anterior abdominal scales (0 = present; 1 = absent)
Character 45. Continuous series of median dorsal scutes extending from skull to dorsal fin (0 = absent; 1 = present)
Character 46. Trunk lateral line (0 = encased in normal interlocking scales; 1 = encased in slender tubes; 2 = encased in noninterlocking scales; 3 = encased in enlarged scutes)
Character 47. Ventral scute series (0 = absent; 1 = present)
Character 48. Ossified supraneurals (0 = present throughout trunk; 1= absent in subdorsal region and anterior caudal peduncle)
Character 49. Caudal cercus (0 = absent; 1 = present)
Character 50. Caudal peduncle scutes (0 = absent; 1 = lateral line, postdorsal fin, postanal fin; 2 = lateral line, paired dorsal, paired ventrolateral, paired ventromedial; 3 = lateral, paired dorsal, large scutes intercalated between lateral series and ventral midline but not organized in distinct series)
Character 51. Dorsal caudal fulcra (0 = one; 1 = more than one)
Character 52. Ventral caudal fulcrum (0 = absent, 1 = present)
Character 53. Pectoral fin spine (0 = absent; 1 = present)
Character 54. Supracleithrum reaching level of extrascapulars (0 = absent; 1 = present)
Character 55. Medial laminar expansion of cleithrum and clavicle forming rear of branchial (opercular) chamber (0 = absent; 1 = present)
Character 56. Cardiac shield (0 = absent; 1 = present)
Character 57. Posterior cleithral notch (0 = absent; 1 = present)
Character 58. Clavicle and cleithrum suture (0 = absent or loose [not interdigitating]; 1 = present, tight and interdigitating)
Character 59. Supracleithral cartilage (0 = absent; 1 = present)
Character 60. Round-based scales (0 = absent; 1 = present)
Character 61. Clavicles (0 = not sutured together; 1 = sutured together)
Character 62. Anterior junction of clavicles (0 = convex; 1 = straight line)

Appendix II

Data Matrix

Below is the data matrix used for our systematic analysis of Acipenseridae. Character numbers and character states correspond to those presented in the list above. N = not applicable; P = polymorphic; U = uncertain homology; ? = unknown. Computationally, "P," "N," and "U" are treated as question marks.

Taxon	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31
Boreosomus	0	1	0	0	0	0	0	1	1	0	0	N	0	1	0	2	0	0	N	N	N	0	0	0	0	0	0	0	?	0	N
Birgeria	0	1	0	0	1	N	0	1	1	0	0	N	0	1	1	2	0	0	N	N	N	0	0	0	0	0	0	0	?	0	N
Chondrosteus	0	1	0	0	0	1	0	1	0	1	?	N	0	1	1	2	1	0	N	N	N	1	0	0	0	0	0	0	?	1	0
Peipiaosteus	0	0	0	0	U	U	U	U	0	0	0	?	0	1	1	2	0	0	N	N	N	1	0	1	1	0	0	0	?	1	0
Polyodon	1	1	1	1	U	U	U	U	0	0	0	0	0	1	1	0	0	1	0	0	0	2	0	2	1	0	0	1	0	1	N
Protopsephurus	1	0	1	1	U	U	U	U	0	1	0	0	0	1	1	0	1	1	?	0	0	1	0	1	1	0	0	1	?	1	0
Priscosturion	0	0	0	0	?	?	?	?	1	0	?	1	0	1	1	2	1	1	1	1	0	2	?	?	?	1	1	0	?	1	0
H. huso	0	1	0	0	0	0	0	0	2	1	1	0	0	0	1	1	1	1	P	0	1	2	1	1	1	1	0	0	1	1	0
Scaphirhynchus	0	0	0	0	0	0	0	0	3	1	1	1	1	0	1	1	1	1	1	1	0	2	1	1	1	1	1	0	1	1	0
P. kauffmani	0	0	0	0	0	0	1	1	2	1	1	0	1	1	1	1	1	1	1	0	0	2	1	1	1	1	1	0	1	1	0
P. hermannni	0	0	0	0	0	0	1	1	2	1	1	0	1	1	1	1	1	1	1	0	0	2	1	1	1	1	1	0	1	1	0
A. brevirostrum	0	0	0	0	1	0	0	0	2	1	1	1	0	0	1	1	1	1	1	0	0	2	1	1	1	1	0	0	1	1	0
A. stellatus	0	0	0	0	0	0	1	1	2	1	1	0	1	1	1	1	1	1	1	0	0	2	1	1	1	1	0	0	1	1	0
A. ruthenus	0	P	0	0	0	0	0	0	2	1	1	0	0	0	1	1	1	1	1	0	1	2	1	1	1	1	0	0	1	1	0
A. fulvescens	0	0	0	0	1	0	0	0	2	1	1	1	0	0	1	1	1	1	1	0	0	2	1	1	1	1	0	0	1	1	0
A. oxyrinchus	0	1	0	0	0	0	0	0	2	1	1	1	0	0	1	1	1	1	1	0	0	2	1	1	1	1	0	0	1	1	0
A. transmontanus	0	0	0	0	0	0	0	0	2	1	1	1	0	0	1	1	1	1	1	0	0	2	1	1	1	1	0	0	1	1	0
A. baerii	0	0	0	0	0	0	0	0	2	1	1	0	0	0	1	1	1	1	1	0	1	2	1	1	1	1	0	0	1	1	0

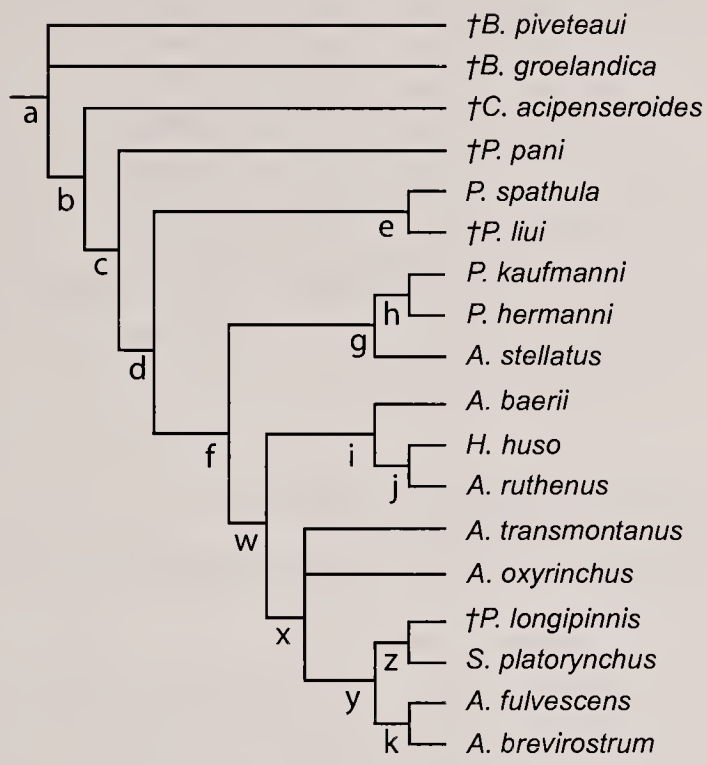
Taxon	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	55	56	57	58	59	60	61	62
Boreosomus	0	0	0	?	0	?	?	?	0	?	0	0	0	0	0	0	?	?	0	1	1	0	0	1	?	0	0	?	0	?	?
Birgeria	0	0	0	0	0	?	?	?	0	?	?	0	1	0	1	0	1	?	0	1	0	0	0	1	0	0	0	?	0	0	N
Chondrosteus	1	0	0	0	1	?	?	?	0	0	0	0	1	0	1	0	1	?	0	1	1	1	0	1	0	0	0	?	0	0	N
Peipiaosteus	1	0	0	2	?	?	?	?	1	1	?	0	1	0	1	0	1	?	0	0	0	0	0	1	0	0	0	?	1	0	N
Polyodon	1	N	0	1	0	0	0	1	1	1	0	1	1	0	1	0	0	0	0	1	1	0	0	0	0	0	0	0	1	1	0
Protopsephurus	1	1	0	0	?	?	?	?	1	1	?	1	1	0	1	0	1	?	0	1	1	1	0	1	0	0	0	?	0	0	N
Priscosturion	1	0	1	1	?	?	?	?	1	1	0	0	1	1	2	0	?	?	2	1	1	1	1	1	1	0	1	?	0	1	?
H. huso	1	0	1	0	1	0	1	1	1	1	0	0	1	1	3	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0
Scaphirhynchus	1	1	1	2	1	1	1	0	1	1	1	0	1	1	3	1	1	1	2	1	1	1	1	1	1	1	1	1	0	1	1
P. kauffmani	1	0	2	2	1	1	1	1	1	1	0	0	1	1	3	1	1	1	3	1	1	1	1	1	1	1	1	1	0	1	0
P. hermannni	1	0	2	2	1	1	1	1	1	1	0	0	1	1	3	1	1	0	3	1	1	1	1	1	1	1	1	1	0	1	0
A. brevirostrum	1	0	1	1	1	1	1	1	1	1	0	0	1	1	3	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0
A. stellatus	1	0	2	1	1	1	1	1	1	1	0	0	1	1	3	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0
A. ruthenus	1	0	1	1	1	1	1	0	1	1	0	0	1	1	3	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0
A. fulvescens	1	0	1	1	1	1	1	1	1	1	0	0	1	1	3	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0
A. oxyrinchus	1	0	2	1	1	1	1	1	1	1	0	0	1	1	3	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0
A. transmontanus	1	0	2	1	1	1	1	1	1	1	0	0	1	1	3	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0
A. baerii	1	0	2	1	1	1	1	1	1	1	0	0	1	1	3	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1	0

Appendix III

Apomorphy Lists

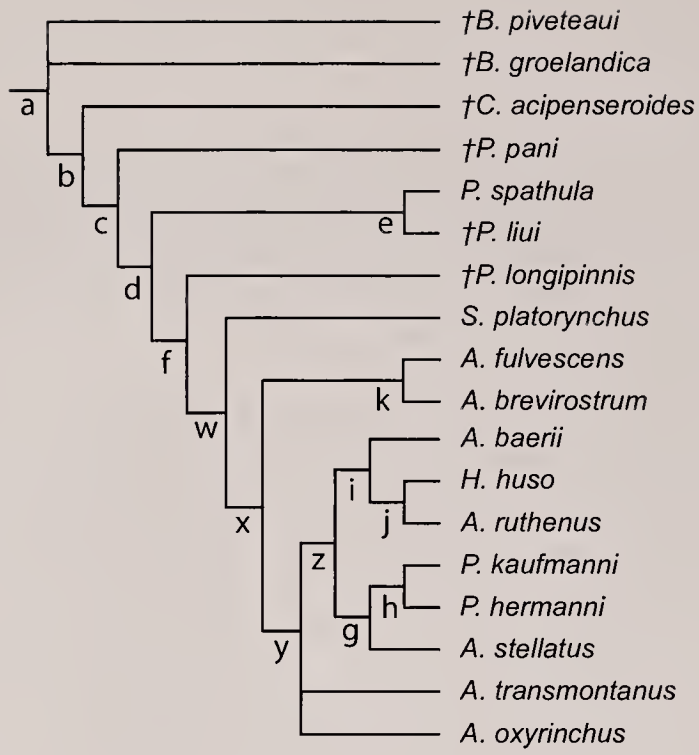
Here we present the complete node support for the two most-parsimonious cladograms (Fig. 128) from the PAUP* analysis of the data matrix provided in Appendix II (under ACCTRAN optimization). Below we list the character number, followed by the state change in square brackets and the consistency index (CI) in parentheses; characters in bold are unambiguous. Note that nodes a through k are the same between the two trees and that nodes w through z are not (also, these labels do not correspond to those used in Figure 129, as indicated by the use of lowercase type).

Tree 1 (see Fig. 128A)



Node a to †*B. piveteaui*: 15 [1→0] (1.00); 44 [1→0] (1.00); 46 [1→0] (1.00)
Node a to †*B. groelandica*: 5 [0→1] (0.50); 52 [1→0] (0.50)
Node a to b (Acipenseriformes): 9 [1→0] (0.75); 10 [0→1] (0.25); 17 [0→1] (0.33); **22 [0→1] (0.67); 30 [0→1] (1.00); 32 [0→1] (1.00);** 36 [0→1] (0.50); 53 [0→1] (0.33)
Node b to †*C. acipenseroides*: 6 [0→1] (1.00)
Node b to c: 2 [1→0] (0.25); 24 [0→1] (1.00); 25 [0→1] (1.00); 35 [0→1] (0.33); **40 [0→1] (1.00);** 41 [0→1] (1.00); **60 [0→1] (0.25)**
Node c to †*P. pani*: 10 [1→0] (0.25); 17 [1→0] (0.33); 35 [1→2] (0.33); **51 [1→0] (1.00); 52 [1→0] (0.50);** 53 [1→0] (0.33)
Node c to d (Acipenseroidei): 16 [2→0] (0.67); **18 [1→0] (1.00);** 22 [1→2] (0.67); 61 [0→1] (0.50)
Node d to e (Polyodontidae): 1 [0→1] (1.00); 3 [0→1] (1.00); 4 [0→1] (1.00); 28 [0→1] (1.00); 33 [0→1] (0.50); 36 [1→0] (0.50); **43 [0→1] (1.00)**
Node e to *P. spathula*: 2 [0→1] (0.25); 10 [1→0] (0.25); 17 [1→0] (0.33); **24 [1→2] (1.00); 48 [1→0] (1.00);** 53 [1→0] (0.33); **55 [1→0] (1.00)**
Node e to †*P. liui*: 22 [2→1] (0.67); 35 [1→0] (0.33); **60 [1→0] (0.25);** 61 [1→0] (0.50)
Node d to f (Acipenseridae): 9 [0→2] (0.75); 11 [0→1] (1.00); 16 [0→1] (0.67); 19 [0→1] (1.00); **23 [0→1] (1.00); 26 [0→1] (1.00);** 29 [0→1] (1.00); **34 [0→2] (0.67);** 37 [0→1] (0.50); 38 [0→1] (1.00); **45 [0→1] (1.00); 46 [1→3] (1.00); 47 [0→1] (0.50); 50 [0→1] (1.00); 54 [0→1] (1.00); 56 [0→1] (1.00); 57 [0→1] (0.50); 58 [0→1] (1.00);** 59 [0→1] (1.00)
Node f to g (Pseudoscaphirhynchinae): 7 [0→1] (1.00); 13 [0→1] (0.50)
Node g to h (*Pseudoscaphirhynchus*): 27 [0→1] (0.50); 35 [1→2] (0.33); 50 [1→3] (1.00); 60 [1→0] (0.25)
Node h to *P. kaufmanni*: 49 [0→1] (0.50)
Node f to w: 8 [1→0] (1.00); 14 [1→0] (0.50)
Node w to i: 21 [0→1] (1.00)
Node i to j (Husinae): 2 [0→1] (0.25); **34 [2→1] (0.67)**
Node j to *H. huso*: 35 [1→0] (0.33); 37 [1→0] (0.50)
Node j to *A. ruthenus*: 39 [1→0] (0.50)
Node w to x: 12 [0→1] (1.00)
Node x to y: 34 [2→1] (0.67)
Node y to z: 9 [0→1] (0.75); **20 [0→1] (1.00); 27 [0→1] (0.50);** 39 [1→0] (0.50); 49 [0→1] (0.50); **50 [1→2] (1.00); 60 [1→0] (0.25);** 62 [0→1] (1.00)
Node z to †*P. longipinnis*: 10 [1→0] (0.25); 14 [0→1] (0.50); 16 [1→2] (0.67); 46 [3→2] (1.00); 47 [1→0] (0.50); 57 [1→0] (0.50)
Node z to *S. platorynchus*: 9 [1→3] (0.75); **13 [0→1] (0.50); 33 [0→1] (0.50); 35 [1→2] (0.33); 42 [0→1] (1.00)**
Node y to k: 5 [0→1] (0.50)

Tree 2 (see Fig. 128B)



Node a to †*B. piveteaui*: 15 [1→0] (1.00); 44 [1→0] (1.00); 46 [1→0] (1.00)
Node a to †*B. groelandica*: 5 [0→1] (0.50); 52 [1→0] (0.50)
Node a to b (Acipenseriformes): 9 [1→0] (0.75); 17 [0→1] (0.33); **22 [0→1] (0.67); 30 [0→1] (1.00); 32 [0→1] (1.00);** 36 [0→1] (0.50); 53 [0→1] (0.33)
Node b to †*C. acipenseroides*: 6 [0→1] (1.00); 10 [0→1] (0.33)
Node b to c: 2 [1→0] (0.25); 8 [1→0] (0.50); **24 [0→1] (1.00); 25 [0→1] (1.00);** 35 [0→1] (0.33); **40 [0→1] (1.00);** 41 [0→1] (1.00)
Node c to †*P. pani*: 17 [1→0] (0.33); 35 [1→2] (0.33); **51 [1→0] (1.00); 52 [1→0] (0.50);** 53 [1→0] (0.33); **60 [0→1] (0.25)**
Node c to d (Acipenseroidei): 18 [1→0] (1.00); 22 [1→2] (0.67); 61 [0→1] (0.50)
Node d to e (Polyodontidae): 1 [0→1] (1.00); 3 [0→1] (1.00); 4 [0→1] (1.00); 16 [2→0] (1.00); 28 [0→1] (1.00); 33 [0→1] (0.50); 36 [1→0] (0.50); **43 [0→1] (1.00)**
Node e to *P. spathula*: 2 [0→1] (0.25); 17 [1→0] (0.33); **24 [1→2] (1.00); 48 [1→0] (1.00);** 53 [1→0] (0.33); **55 [1→0] (1.00); 60 [0→1] (0.25)**
Node e to †*P. liui*: 10 [0→1] (0.33); 22 [2→1] (0.67); 35 [1→0] (0.33); 61 [1→0] (0.50)
Node d to f (Acipenseridae): 9 [0→1] (0.75); 11 [0→1] (1.00); 12 [0→1] (0.50); 19 [0→1] (1.00); 20 [0→1] (0.50); 23 [0→1] (1.00); **26 [0→1] (1.00);** 27 [0→1] (0.33); 29 [0→1] (1.00); **34 [0→1] (0.67);** 37 [0→1] (0.50); 38 [0→1] (1.00); **45 [0→1] (1.00);** 46 [1→2] (1.00); **50 [0→2] (1.00); 54 [0→1] (1.00); 56 [0→1] (1.00); 58 [0→1] (1.00);** 59 [0→1] (1.00)
Node f to w: 9 [1→2] (0.75); **10 [0→1] (0.33); 14 [1→0] (0.50); 16 [2→1] (1.00);** 46 [2→3] (1.00); **47 [0→1] (1.00); 57 [0→1] (1.00)**
Node w to *S. platorynchus*: 9 [2→3] (0.75); **13 [0→1] (0.50); 33 [0→1] (0.50); 35 [1→2] (0.33); 39 [1→0] (0.50); 42 [0→1] (1.00); 49 [0→1] (0.50); 62[0→1] (1.00)**
Node w to x: 20 [1→0] (0.50); 27 [1→0] (0.33); 50 [2→1] (1.00); 60 [0→1] (0.25)
Node x to k: 5 [0→1] (0.50)
Node x to y: 34 [1→2] (0.67)
Node y to z: 12 [1→0] (0.50)
Node z to i: 21 [0→1] (1.00)
Node i to j (Husinae): 2 [0→1] (0.25); **34 [2→1] (0.67)**
Node j to *H. huso*: 35 [1→0] (0.33); 37 [1→0] (0.50)
Node j to *A. ruthenus*: 39 [0→1] (0.50)
Node z to g (Pseudoscaphirhynchinae): 7 [0→1] (1.00); 8 [0→1] (0.50); 13 [0→1] (0.50); 14 [0→1] (0.50)
Node g to h (*Pseudoscaphirhynchus*): 27 [0→1] (0.33); 35 [1→2] (0.33); 50 [1→3] (1.00); 60 [1→0] (0.25)
Node h to *P. kaufmanni*: 49 [0→1] (0.50)
Node y to *A. oxyrinchus*: 2 [0→1] (0.25)

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